VOLUME II. No. 3 JULY, 1954

THE BRITISH JOURNAL OF ANIMAL BEHAVIOUR

Official Journal of the Association for the Study of Animal Behaviour

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The Role of Scent as a Nectar Guide for Honeybees on Flowers and an Observation on the Effect of Colour on Recruits

By NIELS BOLWIG

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It has been suggested that insects are not only guided to the nectar of flowers by visible nectar guides, but also by scent tracks on the petals. Von Frisch (1919, 1923) has proved that scent aids honeybees in their search for food; either they have learned to associate a certain scent with food or during recruitment by dancing bees in the hive. His experiments, however, only show that the bee recognises the species of flower by the scent. They give no indication of the importance of scent as a guide to the bee after it has landed on the flower. It has been shown by Knoll (1926), Zerrahn (1933) and others, that the shape of a flower is of no importance to the bee in recognising it, while its colour is recognised from a distance. Knoll (1926) found that other insects also see the colour from a distance, but, like the honeybee, recognise the flower at short range by the scent. Damaged flowers may also be visited by insects, and a bee can learn to find its way to the nectar of flowers from which the petals have been removed (Giltay, 1904). Where, however, the nectar is concealed in the flower, nectar-guides in the form of lines or dots guide the insects thither (Knoll, 1926; Bolwig, 1938). The work of Jorgensen (1939) indicated that scent also guides the bees within the flowers of *Helenium* and *Centauria*.

To obtain further evidence on the role of scent as a nectar or pollen guide the following experiments were carried out.

Experiment 1

About 25 bees were trained to drink sugar water sprinkled on a glass plate under which was placed a blue disc with a diameter of 14 cm. After training, a similar arrangement, but without sugar water, was placed a short distance away from the training arrangement. In this and in subsequent experiments the positions of the two arrangements were repeatedly changed, so that the bees could not learn them. The number of bees investigating the middle and the edge of the paper without sugar water were counted. Most of them did not settle on the glass over the paper, but they hovered and dipped when they came to the part to which they were attracted. When any bee did settle, all those landing next to it were not counted, because bees in doubt are strongly inclined to settle next to others and form clusters. Of 100 bees which were counted, 96 investigated the edge of the disc, 4 the middle of it.

Experiment 2

The glass plates over the papers were now removed, and scent-tracks of lavender water were drawn across one paper disc (Fig. 1), the other paper being sprinkled with sugar water.

Of 100 bees which investigated the coloured paper with scent tracks, 95 went to its edge.

Experiment 3

Marked bees, which had been trained to collect on paper with lavender scent, were tested on a paper on which radiating scent tracks were drawn (Fig. 1). This paper was placed between the hive and the feeding place. All recruits visiting this paper were observed.

The edge of the paper again attracted the bees more than the centre, but as they flew all over it and settled at random counting was not possible. The bees did not seem to follow the drawn scent tracks. The same observation was also made when trained bees were tested.

Experiment 4

It was of interest at this stage to see how the bees would react to petals with an uneven distribution of scent. Unfortunately, the quick dessication of flower petals made them unfit for experiments, and it was necessary to substitute paper models.

Fifteen bees were trained to drink from a glass sheet, sprinkled with sugar water and

Eau de Cologne, under which was a piece of blue paper. After training, they were offered a glass sheet under which was a 7 cm. long model of a blue petal (Fig. 2a). On the glass above one end of the petal was placed a drop of Eau de Cologne. Out of 100 single visits to the two ends of the 'petal,' 92 were to the scented end.

Experiment 5

Six 'petals' were now put together under a glass plate to form a 'flower' (Fig. 2b), and a drop of Eau de Cologne was placed over its centre. Out of 100 single visits, 87 were to the centre of the 'flower.'

Experiment 6

The result of experiment 5 need not necessarily be due to the scent as the centre of this flower model would produce the greatest flickering effect on the eye of the bee and therefore be the most visible part (Bolwig, 1938).—In the next experiment the scent droplets were placed over the peripheral tips of the 'petals.' Out of 100 single visits, 90 were then made to the scented tips.

Thus the known scent drew the bees to the scented part of the flower model.

Experiment 7

A few *Calliopsis* were growing in the garden where the experiments were carried out. None of these yellow Composites were visited by the bees.

A hole just big enough to squeeze a *Calliopsis* flower through was cut in a sheet of white cardboard. In this hole was fastened a flower from which all petals but one were removed, and the centre of the flower was covered with strips of paper to make it invisible from the air. The petal was trimmed at its distal end to

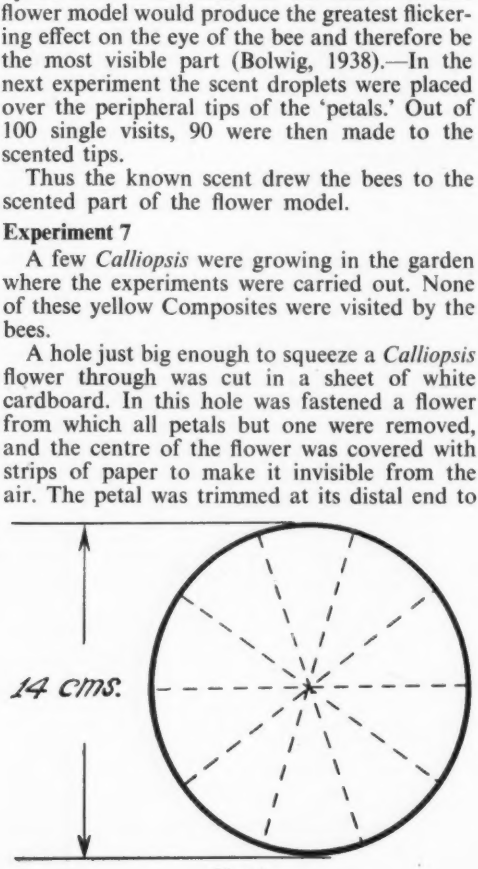

Fig. 1

Fig. 2

give it a symmetrical shape, and a ball of gauze of the same size as the centre of the flower was placed at its tip. The gauze was also covered with a strip of paper, so that approaching bees could not see which was the centre and which was the periphery of the flower.

About ten marked bees were now trained to drink sugar water sprinkled on some *Calliopsis* flowers which had been placed in a bottle of water behind a bush, so that the bees did not see them until they had rounded the bush and were within a distance of a foot or two. After this training, the cardboard with the changed flower was placed in front of the bush, where the approaching bees would see it. The behaviour of every recruit visiting the flower on the cardboard was observed. New bees arriving on the flowers with sugar water were distinctively marked and thereafter no longer considered as recruits. On only two occasions did bees which had once found the flowers with sugar water return to the arrangement on the cardboard. Out of 40 recruits visiting the exposed petal on the cardboard, 38 went to its base.

Experiment 8

To rule out the possibility of nectar guides invisible to man the petal of the flower used for the experiments was substituted by one of yellow paper. With this arrangement 39 out of 40 bees investigated the base of the 'petal.' It therefore seemed certain that bees were guided only by the scent of the disc florets in the centre of the flower.

Experiment 9

During Experiments 7 and 8 it was noticed

that most recruits approached the centre of the flower from the side of the petal. To test this observation a number of bees were trained to drink sugar water from a bluish green sheet of paper scented with lavender. This was done behind a bush, out of sight of the hive. In front of the bush was a watch-glass with lavender scent, bridged over by a piece of cardboard. At one entrance to the scent was a piece of blue paper. To avoid asymmetry in the experiment the blue paper was repeatedly changed from one side to another. With the blue paper to the left 9 out of 13 recruits approached the scent from that side; with blue to the right 10 out of 12 went to it.

Unfortunately the bees became very unruly during this experiment. This made good observations difficult. The results were, however, supported by a further experiment of a similar nature where the scent was experienced in connection with sugar water by most bees but where the colour at the entrance was unknown to them in this connection. Out of 60 bees in this experiment 39 approached the scent from the side of the coloured paper.

Conclusion and Summary

The above experiments show that in flowers without nectar guides, such as *Calliopsis*, certain well-defined, strongly scented parts can guide the visiting bee even when it is without previous experience of the flower.

1. Bees trained to drink sugar water from a coloured disc preferred to seek for their food at its edge. They did not distribute themselves along scent tracks (made with lavender water) on the disc, even if they had been trained to lavender water.

2. Bees trained to Eau de Cologne were attracted to the one end of a paper 'petal' on which a drop of the scent had been placed. This also happened when six 'petals' were arranged to form a 'flower', whether the scent was placed at the centre or at the circumference of this 'flower.'

Untrained bees were more attracted towards the inner than the outer end of a petal left attached to the centre of an otherwise depetalled *Calliopsis* flower. The centre of the flower in the experiment was covered and made invisible to the approaching bee. The same result was obtained when the petal was replaced by one of yellow paper. This rules out the possibility of invisible nectar guides in this flower.

Although the experiments do not disprove the suggestion that scent-tracks may be present on flower petals, they show that it is improbable that any such tracks are of importance to honeybees.

Recruits were found to pay a greater attention to coloured objects than to those blending with the surroundings. On approaching a scent they seemed to prefer to land on a coloured piece of paper placed next to it. This behaviour is of importance to the bees when in search for food.

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Notes on the Mating Behaviour of *Nemobius sylvestris* (Bosc) (Orth., Gryllidae).

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Introduction

The following laboratory observations on the mating behaviour of *Nemobius sylvestris* were made during the course of a study of the ecology of this species. As they differ in some respects from other published accounts of this very easily maintained species, it seems worth describing the process in some detail.

Lespés (1855), Gerhardt (1921), Zacher (1926) and Roland (1947) give accounts of this process, it being left to Richards (1952) to provide the first detailed study of the mating behaviour. The present account draws freely on his observations.

This species is peculiar in that two spermatophores are produced successively, a fact which is not recorded in the papers of continental workers (except possibly Gerhardt (1921)—see later) nor in observations on related American species (Fulton, 1931). Through the good offices of Professor L. Chopard (Paris) and Professor R. Hovasse (Clermont-Ferrand) it has been possible to obtain continental specimens of *N. sylvestris* and these insects show no difference in behaviour from the British specimens. It appears therefore that the double production of spermatophores has been overlooked in this species.

Throughout the following description the terms Stage I and Stage II will be used to describe the events which accompany the production and the disposal of (I) the first spermatophore and (II) the second spermatophore.

Each stage may, quite arbitarily, be subdivided into a number of phases, this being done merely to facilitate the description. The approximate length of time of each stage or phase is indicated, where possible, in parenthesis.

Stage I

Phase I. In the male the appearance of the spermatophore is preceded by a number of body movements.

1. The elytra are raised and intermittent stridulation occurs, the insect usually remaining stationary.

2. The antennae, while in or near the vertical position, are rapidly but intermittently vibrated.

3. The entire body is irregularly jerked backwards and forwards.

Each of these movements may occur singly or in combination. It may be noted that the production of the spermatophore is independent of the presence of the female (cf. Richards, 1952).

Phase II. While the behaviour of the male towards the female is basically one of attraction, in this phase and in the preceding phase, the female is "discouraged" from mounting the male. When a female approaches a male or when a male locates a female, the male turns his abdomen to her and performs the body movements described in Phase I. If, however, the female makes any attempt to mount the male then she is pushed away by his metathoracic legs.

Phase III. 1. The behaviour of the male towards the female becomes passive and no attempt is made to prevent the female mounting.

2. The body movements become violent and more and more exaggerated.

3. The female approaches the male and flicks her antennae over the abdomen of the male. (Phases I-III 20-35 minutes in all).

Phase IV. (a few seconds).

1. The female mounts the male over his lowered cerci and his stridulation drops to a soft fluttering note.

2. The male closes his elytra and pushing back and underneath the female, arches and raises his abdomen. The male genital organ ejects the spermatophore into the opening between the sub-genital plate and the ovipositor of the female.

3. The pair separate, the male jerking away forward from underneath the female.

Phase V. (5-15 minutes).

1. The male again develops the body movements but no stridulation has been observed during this or the following phases.

2. The male does not "discourage" the female from mounting again. This she may or may not

do. If she mounts then she carries out "feeding" movements.

The use of the word "feeding" needs clarification. The males of certain species of the Orthoptera possess special glands which attract the female at the time of copulation (see general treatment of this subject in Chopard, 1938). In certain American species of *Nemobius*, the function of the proximal internal spine of the male hind tibia is that of an alluring gland similar in function to the metanotal gland of *Oecanthus* species.

These glands secrete an alluring substance and the female partakes of this exudate. Gerhardt (1921) and Zacher (1926) describing the same behaviour in *N. sylvestris* use the word "licking"; Richards (1952) uses "feeding."

The female "feeds" in this species by running her labial palps over most of the surface of the right tegmen of the male (see Fig. 1). The mandibles are not used. Clusters of fine hairs are associated with this area (Richards, 1952) and it is suggested that these hairs either secrete a substance or hold a substance secreted by a more remote gland. The presence or absence of secretory or glandular areas with the above described function has not been established morphologically for this species.

Phase VI. (10-15 minutes).

1. The male now "discourages" the female from mounting, and even pursues her. Pursuit of the female may last as long as 15 minutes.

2. The body movements of the male gradually become more and more intermittent.

3. After a time (30-60 minutes) the female rids herself of the spermatophore by either kicking it off by the use of her hind legs or by scraping it along the ground by depressing her abdomen. She then eats it. Stage I passes invisibly into Stage II.

Stage II

Phase I. (5-15 minutes).

1. The male eventually becomes motionless and remains so until the second spermatophore is extruded from the tip of the abdomen. It is larger than the first spermatophore.

Phase II. (20-30 minutes).

1. During this phase and in the preceeding one the female is "discouraged" from mounting the male.

2. After the spermatophore has been produced the body movements begin (see Fig. 2).

Phase III.

1. The male does not "discourage" the female from mounting and his body movements become more violent and more exaggerated. The female approaches the male.

The copulatory and post-copulatory phases follow, closely resembling those described in Stage I (see Fig. 3).

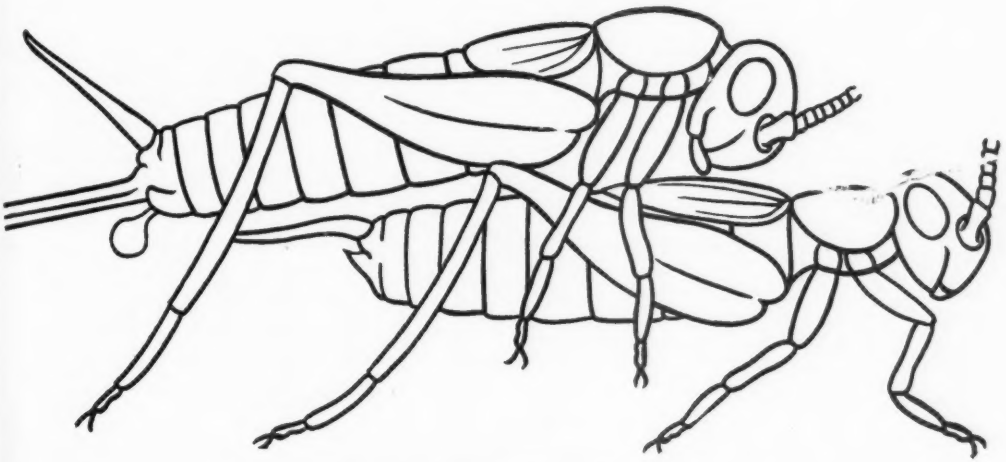

Fig. 1. Female "feeding" on the male after copulation in Stage 1. Note the first spermatophore on the female.

Comparison of the Stages

It is to be noted that there are differences between Stage I and Stage II, not only of behaviour patterns but also of a difference in the size of the respective spermatophores. It has been possible to remove and measure the first and second spermatophore after the completion of each stage. The average diameter of the ampulla of the first spermatophore was 0.303 mm. (σ_{11}=0.0025), that of the second spermatophore was 0.946 mm. (σ_{28}=0.016) (see Fig. **4**).

Gerhardt's (1921) measurements of the "genuine" spermatophore are roughly similar to those given above for the second spermatophore. His measurements on the "Pseudospermatophoren" do not correspond with the above data for the first spermatophore. A number of other anomalies exist between Gerhardt's observations and those set down here which make it impossible, at the present, to correlate the two sets of data.

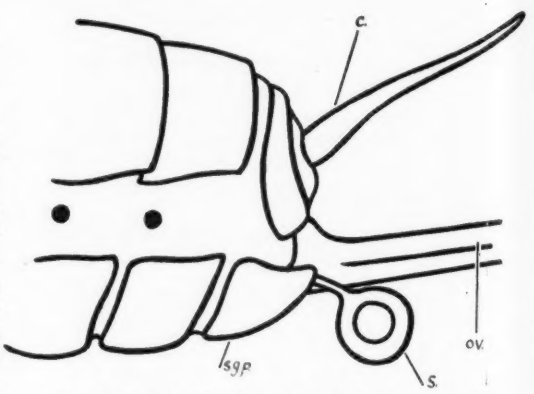

Fig. 3. Female-side view of the posterior region to show the insertion of the spermatophore (Stage II).
c.—cercus. ov.—ovipositor.
s.—spermatophore. s.g.p.—sub-genital plate.

The main difference in behaviour between the two stages lies in the fact that the second spermatophore is produced without either stridulation or the violent movements of the body and antennae. Except for this fact both stages follow very similar courses; during each the same body movements occur, as does also the change in behaviour of the male to the female before and after copulation. It may be that the "discouraging" behaviour prevents copulation until the spermatophore has hardened (cf. Fulton, 1931).

General Observations

When the male failed to effect a transfer of a particular spermatophore then he scraped it off and ate it. With a failure in Stage I the second

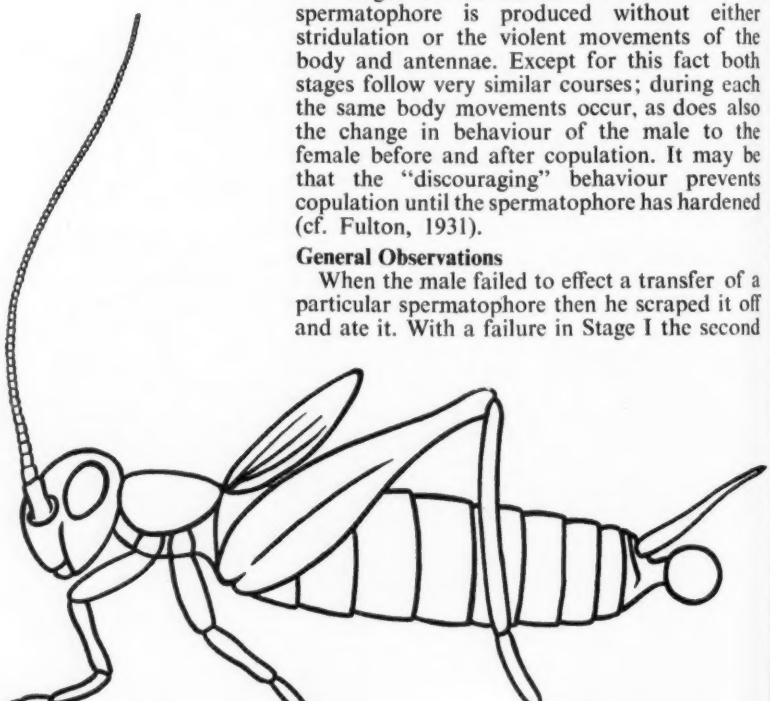

Fig. 2. Side view of male in Phases II-III of Stage I, to illustrate the body movements.

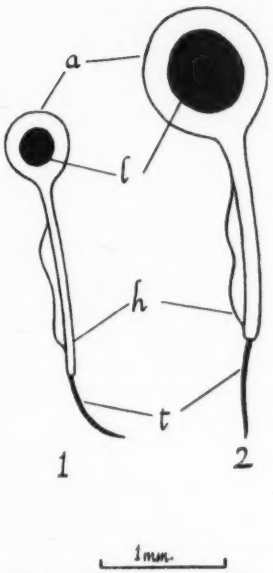

Fig. 4. Spermatophores 1 and 2.
a.--ampoule. h.—handle. l.—lumen. t.--tube.

spermatophore was never produced and the next spermatophore was of the Stage I type. Failure in Stage II produced a Stage I at the next mate. This substantially supports Richard's suggestion that the stimulus for the male for the development of Stage II is a successful completion of Stage I. (see Fig. 5).

It is interesting to speculate on the stimulus which triggers the female behaviour for mating. Richards observed one male devoid of functional elytra which was able to mate successfully. During the present observations three such males were watched and seven others in which the antennae were reduced to only 2-5 segments (normal number of segments in the antennae of adults being from 100-130). All were able to mate freely. It is possible then that the jerking of the body is the primary stimulus for the female in the pre-copulatory phases once the male is in her range of vision. The stridulation may serve to attract the female within this range (Haskell, 1953). However, Khalifa (1950) suggests that touch, not the senses of sight or smell, are important in the analogous process in *Gryllus domesticus*.

Richards (1952) records that "feeding" may or may not occur after the copulations in Stage I and Stage II. In Stage I "feeding" occurred in 6 out of 19 cases; in Stage II in 19 out of 52 cases. This observed incidence of "feeding" is particularly interesting from the point of view of its significance. Gurney (1947) suggests that the function of certain special glands in the male of some species of the Orthoptera is to provide an attraction to the female so that she does not eat the spermatophore before the sperm mass has passed into the spermatheca. The observations recorded here suggest that this may not be the case in this species. After the female has

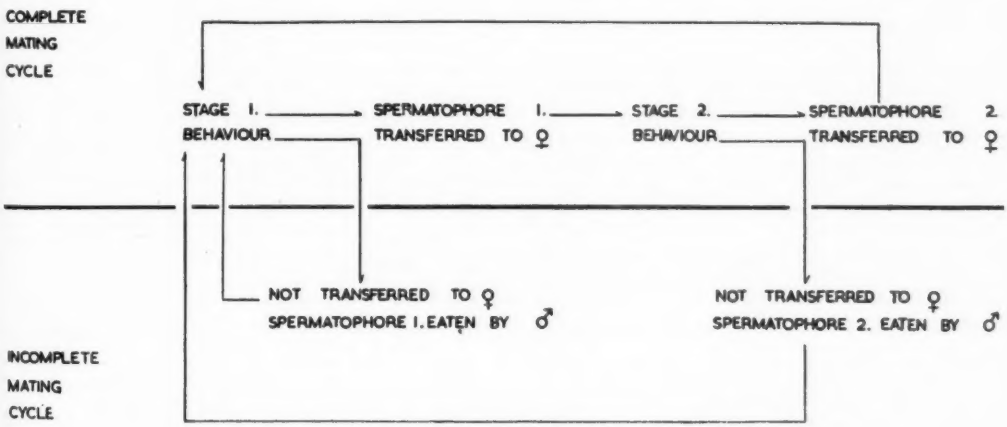

Fig. 5. To show the cycle of events in complete and incomplete matings of both Stages.

"fed", some 30-50 minutes elapse before the spermatophore is scraped off and eaten. In those females in which "feeding" has not taken place, 30-60 minutes elapse before the spermatophore is removed. This suggests that the act of "feeding' does not affect the time at which the spermatophore is eaten.

In the light of the above facts it is interesting to speculate on the function of "feeding" in this species. It has already been noted that the presence or absence of a gland or a secretory area has not been determined. If on examination a gland is found to be present then Gurney's hypothesis is not strictly applicable to this species. The absence of a gland, on the other hand, might suggest that "feeding" may be a relic deriving from some ancestral behaviour. (cf. Khalifa, 1950).

Khalifa (1950)* in his work on the sexual behaviour in *Gryllus domesticus* has observed a "watching" behaviour, on the part of the male which may or may not safeguard against the destruction of the spermatophore by the female. An analogy between "feeding" and "watching," as regards function is obvious but the significance of these behaviour patterns requires further elucidation.

From the biological point of view the production of two spermatophores is interesting. Several questions remain at the moment unanswered. Do the two stages represent one combined or two actual copulations? Observations in the field suggest that due to the "discouraging" behaviour in Phase IV of Stage I it seems unlikely that the same female receives both spermatophores. Are either of the spermatophores non-functional from the point of view of a successful fertilisation?

If time allows, it is hoped to elucidate the above problems in further research.

* In this paper the author states that Fulton (1931) observed a female *Nemobius sylvestris* "entertained by a milky secretion obtained from a spine on the male's hind tibia," (p. 272). No such spine exists on *N.sylvestris* and this species was not among those studied by Fulton; his attention was confined to the American species only.

Acknowledgments

I wish to express my gratitude to Professor L. A. Harvey and to Mr Ian Linn for their helpful advice during the preparation of this manuscript. I am also indebted to Mr T. J. Richards for many pleasant and stimulating conversations; to Professor B. B. Fulton for information on the American species of certain Orthoptera; and to Professor L. Chopard and Professor R. Hovasse for their co-operation in sending me living specimens of *N. sylvestris*.

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Relations Between the Central Nervous System and the Peripheral Organs*

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The relation of the Central Nervous System (CNS) to the peripheral senses and muscular movement is an old and much discussed problem. Here we are at the heart of the physiology of behaviour, and in comparison to that which is not known, our present knowledge is very meagre and vague ! Under these circumstances, our knowledge and conceptions are dependent upon the method which happens to be popular at the moment. In this field, the method which has played the greatest role consists of, first, artificially inactivating the CNS and then, through peripheral stimulation, evoking a particular response. On this basis, the CNS is often held to be only a reflex-mechanism, yet we know today that this view is one-sided. In order to be in co-ordinated activity, the CNS often needs a minimum of stimulation or loading by afferent impulses; the conception of chain-reflex-co-ordination has been recognised almost everywhere as being incorrect. Isolated, that is de-afferented, parts of the nervous system show continued electrical activity. One can therefore say that, as a rule, deafferented ganglion cells, under otherwise normal conditions, possess "automaticity."

These facts allow us to regard the function of the peripheral senses from a new viewpoint. The classical reflex-concept assumes that the peripheral stimulus initiates the central nervous activity. Since we now know that this supposed cause is often unnecessary, it is possible to start from the CNS. We can ask the question, what effect is produced on the sensory-receptors by the motor impulses which initiate a muscular movement? Thus, we look from the opposite direction, not from the outside inward, but from the centre to periphery. You will quickly see that in this manner we shall come upon new problems and experimentally verifiable hypotheses.

In order to make myself clear, I should like first to explain a few terms. The whole of the impulses which are produced by whatever stimuli in whatever receptors I shall term *afference*, and in contradistinction to this I shall call the whole of the motor impulses *efference*. Efference can only be present when ganglion cells are active; afference, on the contrary, can have two quite different sources: first, stimuli produced by muscular activity, which I shall call *re*-afference; second, stimuli produced by external factors, which I shall call *ex*-afference. Re-afference is the necessary afferent reflexion caused by every motor impulse; ex-afference is independent of motor impulses.

Here are some examples: when I turn my eyes, the image present on the retina moves over the retina. The stimuli so produced in the optic nerve constitute a re-afference, for this is the necessary result of my eye movement. If I shake my head, a re-afference necessarily is produced by the labryinth. If, on the other hand, I stand on a railway platform looking straight at a train when it starts to move, the moving image on the retina of my unmoving eye produces an ex-afference; likewise, when I lie in a tossing ship, the impulses of my labyrinth will constitute an ex-afference. If I shake the branch of a tree, various receptors of my skin and joints produce a re-afference, but if I place my hand on a branch shaken by the wind, the stimuli of the same receptors produce an ex-afference. We can see that this distinction has nothing to do with the difference between the so called proprio- and extero-receptors. The *same* receptor can serve both the re- and the ex-afference. The CNS, must, however, possess the ability to distinguish one from the other. This distinction is indispensable for every organism, since it must correctly perceive its environment at rest and in movement, and stimuli resulting from its own movements must not be interpreted as movements of the environment. I want to describe experiments which show how the CNS distinguishes between ex-afference and re-afference.

When one rotates a striped cylinder around a

* Lecture delivered at the Zoological Laboratory, Cambridge, on 30th October, 1953.

quietly sitting insect, for instance the fly Eristalis, the animal turns itself in the same sense (Fig. 1a). This is a well-known optomotor—"reflex." As soon as the animal moves itself, for instance, "spontaneously" (or stimulated by a smell), one observes that it turns itself unhindered by the stripes of the stationary cylinder. We must ask ourselves why the animal at every turn is not turned back by his optomotor "reflex," since the movement of the image on the retina is the same as in the first

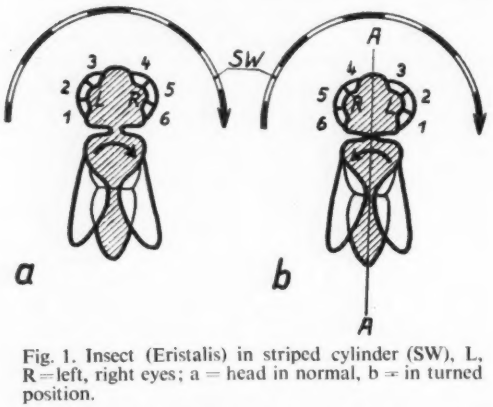

Fig. 1. Insect (Eristalis) in striped cylinder (SW), L, R = left, right eyes; a = head in normal, b = in turned position.

case, when the cylinder moved and the animal was stationary. A possible answer according to the reflex - theory is that in locomotion the optomotor-"reflex" is inhibited or "blocked." But we shall see that this answer is incorrect. It is possible, as has been shown by my colleague Mittelstaedt, to turn the head of the insect through 180° about the long axis (Fig. 1b A-A); then the head is fixed to the thorax, so that the two eyes are effectively interchanged and the order of the visual elements is reversed. The unmoving animal now responds, when the cylinder turns to the right, by turning itself to the left, as is to be expected from the reversed position of the eyes. If it is indeed the case that in spontaneous (or otherwise caused) locomotion the optomotor-reflex is "blocked," the animal should move *un*hindered in the stationary cylinder. But the opposite is the case; once the insect begins to move, it spins rapidly to right or left in small circles until it is exhausted. We have observed the same behaviour with fishes, whose eyes have been turned 180° about the optic axis. But we have found this behaviour only in patterned optical surroundings; in optically homogeneous surroundings the animal moves normally. This indicates that the optomotor-"reflex" is not "blocked" in locomotion, but on the contrary, the associated re-afference plays an important role. Exactly what that role is will be made clearer by the next example.

If a vertebrate is turned over on its side by external forces, the well-known righting "reflexes" are initiated by the ex-afference of the labyrinth. But, just as in my first example, every animal is able to take up any position without righting reflexes being produced by the re-afference of the labyrinth. Again, it has been believed that the reflexes were "blocked" during position changing; and, again, we can show that this is not the case.

The righting reflexes, as is well-known, are released by the statoliths in the labyrinths, which, when the head is tilted, produce a shearing force on the underlying sensory organ, as we have found in fishes. One can increase this mechanical force which the statoliths exert on the sense organs, through the addition of a constant centrifugal force. We have built for this purpose a small revolving laboratory, capable of more than doubling the gravitational force. In this manner the statolith is made heavier, and the corresponding shearing stimuli produced by every tilting of the head are quantitatively increased. If one records the tilting of free swimming fish under these conditions, one finds that the degree of tilting becomes proportionally less, the heavier the statoliths are made. (For the method of measurement see v. Holst u. Mittelstaedt, 1950). If the statoliths are removed, then the behaviour of the fish is the same under normal and centrifugal conditions. We see, therefore, that the re-afference of the labyrinth is not "blocked", but has a quantitative effect upon the *degree* of tilting, and, indeed, the greater the re-afference, the smaller the degree of the movement. One can say that the CNS "measures" the degree of movement by the magnitude of the re-afference thereby released.

Thus we have learned two facts: if the form of the re-afference is reversed, as in the first example, than the initiated movement is increased progressively. Secondly, if the re-afference keeps its normal form but is increased, as in the second example, the initiated movement is correspondingly decreased. These facts allow us to formulate a hypothesis about the

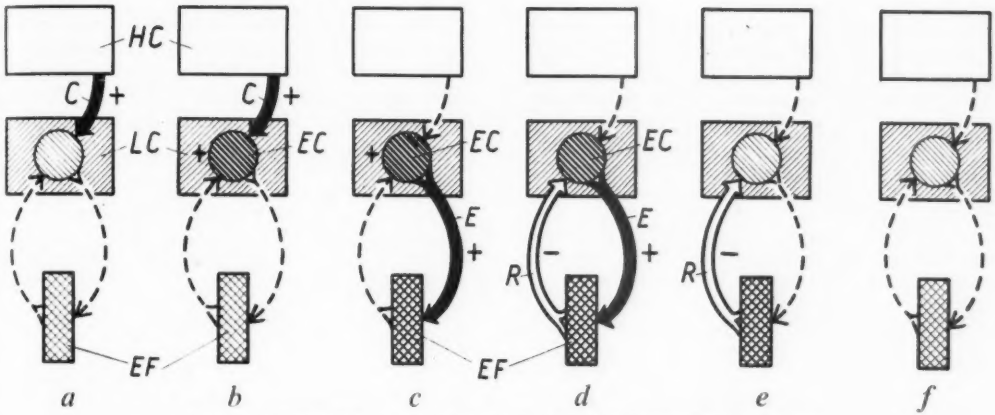

Fig. 2. Illustration of the re-afference principle; see explanation in text.

mechanism here involved. We shall propose that the efference leaves an "image" of itself somewhere in the CNS, to which the re-afference of this movement compares as the negative of a photograph compares to its print; so that, when superimposed, the image disappears. Figure 2 illustrates this in a number of subsequent steps. A motor impulse, a "command" C (Fig. 2a), from a higher centre HC causes a specific activation in a lower centre LC (Fig. 2b), which is the stimulus-situation giving rise to a specific efference E (Fig. 2c) to the effector EF (i.e. a muscle, a joint, or the whole organism). This central simulus situation, the "image" of the efference, may be called "efference copy," EC. The effector, activated by the efference, produces a re-afference R, which returns to the lower centre, nullifying the efference copy by superposition (Fig. 2d-f). Because of the complementary action of these two components we can arbitrarily designate the whole efferent part of this process as plus (+, dark coloured) and the afferent part as minus (—, white coloured). When the efference copy and the re-afference exactly compensate one another, nothing further happens. When, however, the afference is too small or lacking, then a + difference will remain or when the re-afference is too great, a — difference will remain. This difference will have definite effects, according to the particular organisation of the system, The difference can either influence the movement itself, or for instance, ascend to a higher centre and produce a perception.

Let us first consider the simple situation of Fig. 2. The initiated movement will continue, until the re-afference exactly nullifies the efference copy. Then we must predict the following: first, if through external influence the re-afference is increased, then the initiated movement will end prematurely. We have already seen that this is the case in the fish labyrinth experiment with the centrifuge. Secondly (Fig. 3a), if the re-afference is inverted, that is changed from — to +, there will be no nullification, but summation (Fig. 3b) and the movement will progressively increase, as we have

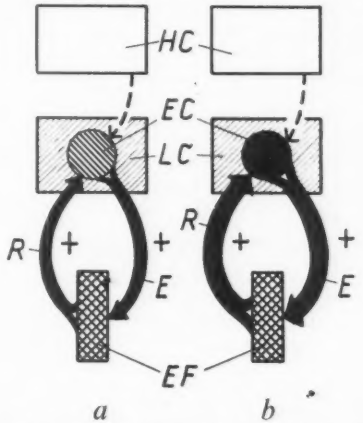

Fig. 3. Illustration of the experiment with the eyes in turned position (Fig. 1); see explanation in text.

already seen in the experiment with the inverted eyes*. Thirdly (Fig. 4), in the case where the re-afference is lacking (for instance, due to the

* This is the so called "positive feed-back."

destruction of the afferent pathways) the initiated movement will not be increased, as in the second case, but will continue until something else limits it. This behaviour occurs widely and

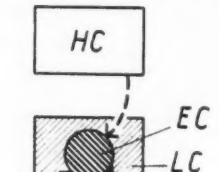

Fig. 4. Illustration of the experiment with interrupted afference; see explanation in text.

can be seen particularly well in fish without labyrinths in optically homogeneous surroundings. Every turning or tilt leads to circling or summersaulting. Also, in the human disease Tabes dorsalis, where the dorsal roots are destroyed, the well known exaggerated, ataxic movements of the limbs indicate that the same mechanism is involved. Therefore, contrary to the chain-reflex theory, the stimulus, originating with every movement, that is the re-afference, produces not an augmenting, excitatory, but a *limiting*, effect on the movement. Only those forms of locomotion, such as the swimming of fish, which do not require a constant adjustment to the surrounding medium, proceed just as before after de-afferentation. These movements are automatically co-ordinated in the CNS and therefore require no limiting re-afference (v. Holst, Lissmann).

With this simple scheme we are able to understand a number of previously unexplained types of behaviour. The most hypothetical part of this theory is the postulated efference copy: this "image" in the CNS, produced by the "command" and matched by the re-afference. I am going to present direct proof of the existence of this phenomenon. For this purpose I choose two human examples, in which the difference between the efference copy and re-afference is transmitted to a higher centre and produces a perception. My first example is concerned with the already mentioned human eye movement.

A re-afference from the actively moving eye can have two sources: firstly, movement of the image across the retina and secondly, impulses from the sensory cells of the eye muscles. The former results in a conscious perception; the latter is of no importance for the following consideration. Consider my eye mechanically fixed and the muscle receptors narcotised (Fig. 5a). When I want to turn my eye to the right, an efference E and, according to the theory, an efference-copy EC is produced, but

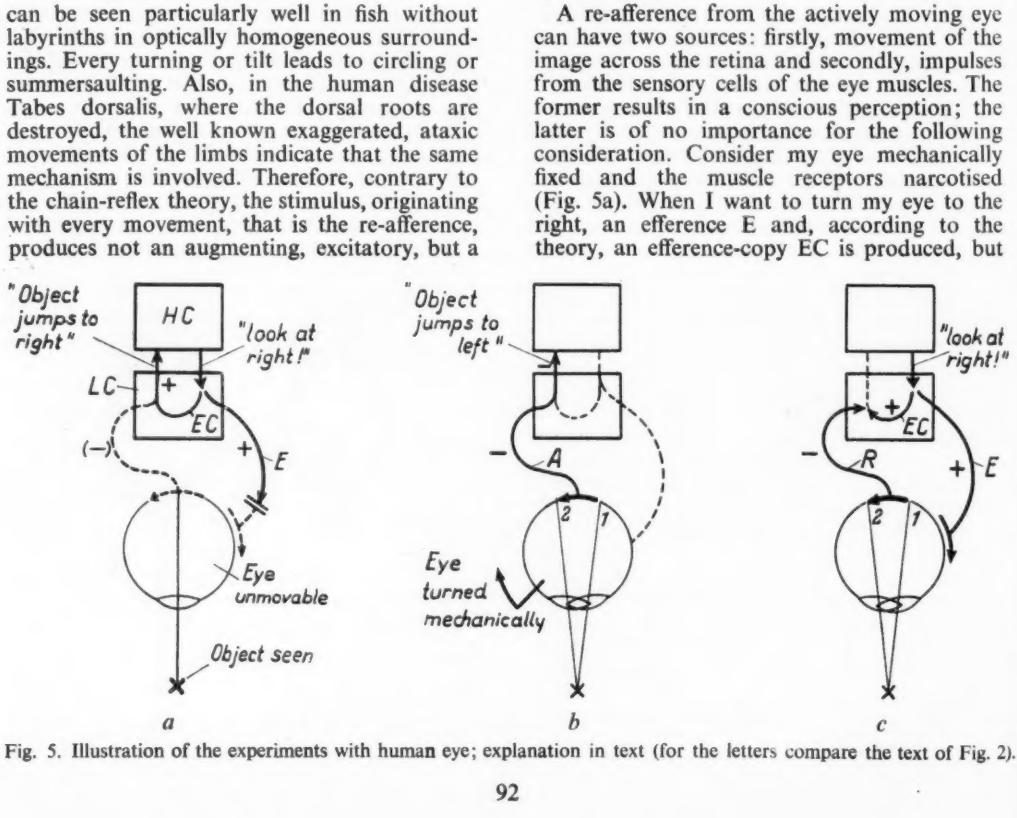

Fig. 5. Illustration of the experiments with human eye; explanation in text (for the letters compare the text of Fig. 2).

the immovable eye does not produce any re-afference. The efference-copy will not be nullified, but transmitted to higher centres and could produce a perception. It is possible to predict the exact form of this perception (v. Holst und Mittelstaedt, 1950). The perception, if I want to turn my eye to the right, must be that "the surroundings have jumped to the right." This is indeed the case ! It has been known for many years from people with paralysed eye muscles and it has been established exactly from the experiments of Kornmuller on himself that every intended but unfulfilled eye movement results in the perception of a quantitative movement of the surroundings in the same direction. Since here *nothing* happens on the afferent pathways, this false perception *can* only result from the activity, originated by the intention of the eye movement, being returned to higher centres. This is another way of saying that the unmatched efference-copy causes the perception.

Now, we make a simple experiment and turn the paralysed eye mechanically to the right (Fig. 5b). In this case both the motor intention and also the efference-copy are lacking, but the image moves across the retina and afference A is transmitted, unmatched by an efference-copy, to higher centres and produces, as is known, the perception that "the surroundings move to the left." This is also a false perception. If now we combine the first case with the second, that is, if my eye is moved mechanically at the same time I intend this movement—which is the same as *voluntarily* moving a *normal* eye—then in fact these two complementary effects just mentioned are produced: firstly, the perception of the returning "command" causing a jump of the surroundings to the right and, secondly, an image-motion on the retina producing a jump of the surroundings in the opposite direction. These two phenomena, the efference-copy and the re-afference, now compensate each other (Fig. 5c); and as a result *no moving* of the surroundings is perceived. The surroundings appear stationary during this normal eye movement, and *this* perception is *physically correct*. As we have already seen, the correct perception results from two opposite and false perceptions which cancel each other. Thus, we understand a phenomenon with which Psychology has been concerned for many years, that is, the perception of the surroundings as nearly stationary during eye movements ("Raumkonstanz").

Now we come to the second example, visual accommodation. The eye is focussed for distant vision when at rest, since the elastic lens is flattened by its zonal fibres. For near-accommodation a circular muscle, working against these fibres, allows the lens to round up. We should also like to apply our theory to this system. If the accommodation apparatus is narcotised, (for instance by atropine), that is, the eye is permanently accommodated for distant vision, than an intention for near-accommodation will start a motor-impulse, which cannot be nullified by any re-afference and, therefore, must return to a higher centre, where it can produce a perception. This is indeed the case. All objects in the visual field become small, and this false perception is called "micropsia." The same phenomenon must exist with a normal eye, if we imprint an after-image of a distant cross on the retina and then look upon a near surface. Since the after-image remains the same size and sharpness on the retina, it must appear very small on the near surface, because again only the "command" for accommodation returns to the centre of perception. This is also the case, as one can easily convince onself. These false perceptions appear, although the *peripheral stimulus-situation* is *un*altered. If, on the contrary, the *accommodation* of a normal eye is *un*altered, that is, if we look first at a small and then at a large cross at the *same* distance, then naturally the changed afference will be transmitted to the centre of perception and we see the second cross to be larger. Now we combine this last case with the first, that is, we observe with a *normal* eye a cross, moving from a distant point nearer to the eye. This initiates the accommodation-impulse, which returning, tells us "the cross is becoming smaller"; but at the same time the enlargement of the retinal image states, "the cross is becoming larger." The two cancel one another out, with the result that we perceive the cross to be of *constant* size. Again, the correct perception is the result of two opposite false perceptions; and, further, we come to an understanding of a phenomenon, long discussed in Psychology, the "GrössenKonstanz der Seh-Dinge" (Hering), which means that we see the objects to be nearly the same size irrespective of their distance from us.

I could present still further examples from man and from lower and higher animals which would show what role the re-afference plays in general in behaviour. It serves either to limit

the magnitude of movement or to insure the constancy of the perceived surroundings during movement, and so makes possible the distinction between real and apparent motion of objects. The first step in both of these functional mechanisms is the comparison of the re-afference with the efference-copy.

In conclusion, permit me a few general considerations. I have attempted to show through the example of this central nervous mechanism, that it is possible in the field of the Physiology of Behaviour to avoid formulating "theories," which are only generalised descriptions of observations; rather should we follow the example of the exact sciences, namely, that a theory must exactly predict what will happen under defined conditions, so that one can by experiment verify or disprove it. Thus one avoids the error of false generalisation, which often occurs in central nervous physiology. For this reason I would like to emphasize that the principle of re-afference is only *one* of *many* central nervous mechanisms. There exists a large number of other mechanisms with other modes of function, and of these we know as yet very little. We recognise fragments of some of them and call them "reflexes"; but this term denotes fragments of very different mechanisms. I believe the whole Central-Nervous System is a "hierarchical system" of such different functional parts, a concept which you find also in Tinbergen's book "The Study of Instinct."

One final point. I have spoken of neither electrical spikes, nor nerve pathways, nor anatomical centres, in which particular functions might be localised. In the realm of behavioural analysis these things are indeed of secondary interest. The functional schemata, constructed in order to illustrate definite causal relationships, are quite abstract, although the consequences they predict are concrete and experimentally verifiable. The physiologist who fully understands such a causal system is still unable to deduce where the cell elements which perform this function are located, or how they operate. Such questions are dealt with at another level of investigation, where the electrophysiologist works and develops his own terminology. It is useful and justifiable for every level of investigation to have its own language, but we must expect, that, with a greater advancement of our knowledge, it will be easy to translate one such language into another. Until such a time, each field must develop along its own lines, unhindered by the many possibilities for misinterpretation.

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The Courtship of the Brown Leghorn Cock

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While comparing the sex drives of several White Leghorn cocks, Guhl (1951) found that although some of the cocks courted the hens at equal rates, the total numbers of crouches received by the cocks differed significantly. The term courting used by Guhl included the waltz, the approach of the cock from behind the hen, the peck-like grasping of the hen, and the placing of the cock's foot on the back of the hen. These actions are only a few of the movements performed by cocks when released with hens, but since Guhl was primarily interested in the rates at which his cocks trod the hens, he paid little attention to their courtship. In the present work the courting behaviour of five Brown Leghorn cocks is described in detail and the relationship between the courting of the cock and the voluntary crouch of the hen is studied.

Materials and Methods

All the birds used in this study were Brown Leghorns. Five sexually experienced cocks from a single inbred line were used. Two (Cocks A and B) were two years old and the others were a year younger; they were identical in plumage and their sizes varied little.

The first phase of the experiment was in the late spring and early summer of 1953, with the second phase in the autumn of the same year. During this second phase all the cocks and many of the hens were moulting, and this period was deliberately chosen to ascertain whether the physiological condition of the birds altered the relationship between the courting of the male and the crouching of the female. Both phases lasted 7 to 8 weeks, but due to the fact that 3 pens of hens were used in phase 1 and only 2 in the second, the total phase time that each cock was observed differed in the two seasons. It was approximately 10 hours in the summer and approximately 7 hours in the autumn. The males were kept in individual cages away from the hens and were released singly into the pens. For the first half of the summer an observation period was 30 minutes but for the rest of the experiment it was 20 minutes. Short observation periods meant that the cocks could concentrate on the hens without the intervention of other drives.

The hens were individually marked by means of coloured rings and any hen nesting or otherwise absent was noted. The roosting perches were closed off during these periods, so that the cock had full access to any female in the pen. The observer was hidden from the birds in the summer phase, but was in full view of them in autumn. A record was kept of all crouches given in both phases, and the male waltzes were recorded over much of the time. For the last third of each phase detailed records of the behaviour of the cocks were kept.

Differences in the Actions Performed by Cocks

Results

The actions performed by these cocks were generally well defined and the majority of them were performed by all the cocks, but at frequencies which were fairly constant for a particular cock. They are described briefly below.

Waltzing

The cock drops one wing and approaches the hen with short shuffling side steps. It is very variable in duration and tempo. Sometimes it is perceptible only because one wing is trailing. There are three types of waltzes distinguished by the occasions on which they are released. The first is given by cocks to hens that are not overtly receptive. The second is given to a hen that has crouched, and the third type is given to the hen that the cock has just trodden. The first type is a display action to which the hen may crouch. Sometimes the male grabs her as he waltzes round her. It also occurs sometimes when two males meet. A dozen contests between cocks were staged on home and neutral territory during this work and in a number of these the dominant cock waltzed to the other cock. It occurred particularly in those cases where the one cock showed no fight at all, and was completely lacking in those cases in which the cocks were evenly matched and both pugnacious. Here a fight usually developed with no preliminary displays. In the fighting context the waltz undoubtedly has display value and it seems that in courtship it is used as a display to stimulate the female to crouch; but here lies an interesting problem. Is it originally a threat display in both contexts ? Tinbergen

& Moynihan (1952) report that the Black-headed gull male acts aggressively towards the female early in the courtship, and cite other similar cases, so that it is possible that the waltz is basically a threat display in both contexts.

The second type of waltz, given in response to the crouching female, is probably of a similar nature to the first type. The third type is much rarer and may be a displacement reaction analogous to the post coitus ceremonies in other birds (Tinbergen, 1952). The possibility however, that this type of waltz may constitute real aggression must not be dismissed entirely. In the ensuing statistical analysis only pre-copulatory waltzes are used. A single waltz was judged finished when the wing was raised.

Tidbitting

The cock pecks at the ground, gives food calls and may scratch the ground for food. Domm and Davis (1948) describe these actions of pecking and scratching as two separate displacement reactions, but here they are treated together, for they appeared to belong to a single action and it was impossible to score them separately. It occurs when the cock is highly motivated and the hens do not crouch. Sometimes, however, cocks tidbit without any display even if the hens crouch to them. In both cases it may be a displacement reaction. In the first one there is an excess of the sexual drive and the drive cannot be consummated, as the requisite external stimuli are missing. In the second case the sex drive is low and is in conflict with another drive, so that an outlet is found in tidbitting. Generally, the movements are very exaggerated and it appears to have different intensities, for sometimes it is accompanied by calls. Often the hens run to a tidbitting cock, and so it can aid the cock in his courtship. Sometimes it can lead to other actions, one of which is dust-bathing. As the cock scratches, the legs become bent and the body is lowered to the ground; the dust-bath then commences, so that in this drive tidbitting may be a displacement reaction of a lower threshold value than dust-bathing. The other action, "cornering," is not so directly related to tidbitting but appears in movement to be similar. The cock runs to a corner, stamps his feet and lowers himself to the ground with movements similar to those in the transition between tidbitting and dust-bathing. Once on the ground he may be still or peck at the ground as is done in dust-bathing. The initial move away from the hens is very striking, but this too may occur in tidbitting. Furthermore, the cock may call as in tidbitting, so that the relationship between the three actions is very marked. In some cases the male does not sit down, but stands in the corner stamping in a jerky manner. It invariably elicits a response from the hens who run to the cock, stand around him, or scratch his back. It appears, therefore, to be another displacement reaction which can aid the cock in his courtship by bringing the hens nearer him. It may have its origin in a nesting habit that has long since disappeared during the course of evolution, or it may be a fleeing movement analogous to that described by Hinde (1953) in the courtship of the chaffinch. Since cornering is a discrete action its scoring was easy. As soon as the cock left the corner it was counted as finished. Tidbitting and dust-bathing were not scored so satisfactorily, but as soon as another action interrupted the tidbitting or dust-bathing, a point was scored.

Wing-flapping

When this action is most vigorously expresse d the cock raises himself to his full height and beats his wings so that they clap. It may, therefore, advertise the presence of the cock both visually and audibly, for the clapping may be heard some distance away. Sometimes a cock will stand right over a hen and wing-flap vigorously; interpreted subjectively this might mean that he is trying to stimulate her or intimidate her into crouching. It is also sometimes seen prior to a cock fight. From these two pieces of evidence it appears to be a display movement of a much lower valency than waltzing, for it seldom elicits the same response in the hens as Waltzing. The series of movements between the raising of the wings and their final folding was counted as one wing-flap in this analysis.

Feather-ruffling

The neck is stretched, the ruff is raised, the other feathers are ruffled and the whole body is shaken. It was described by Skard (1937) as a male approach of weak intensity. Its occurrence in mating is of regular but low frequency. It can occur as an isolated action or it can follow copulation, but it does not seem to have such a clear cut relationship as Skard attributes to it. Possibly it is a displacement reaction or a vestigial display action, for the raising of the ruff may have had some value in the past history of the species. One feather-ruffling was scored as soon as the ruff and body feathers were lying flush again.

Tail-wagging

The tail is moved rapidly from side to side in the horizontal plane. This series of movements until the tail stopped constituted one tail-wag.

Head-shaking

The head is tilted to one side and vigorously shaken with circular movements. In the ensuing analysis one head-shake consisted of a series of such movements until the head came to rest.

Preening

This action can often be a displacement reaction in many species of birds (Tinbergen 1951). The fact that during this work it occurred in such short observation periods, albeit at low frequencies, favours its being a displacement reaction.

Tail-wagging and head-shaking are also considered to be displacement reactions, occurring when the cock could not get the requisite response from the hens.

Strutting

The cock runs about with his legs slightly bent and the wings drooped, so that the tips of the primary feathers sometimes nearly touch the floor. The neck is retracted slightly. The movements are sometimes jerky. It may be an intention movement from the bow made preparatory to jumping, and thus similar in origin to the display of the turkey cock (Daanje 1950). It often leads to the cock chasing the hens and may have some ritual value in the courtship but since one successful cock never strutted it cannot be essential as a social signal to the hens.

Sex-calling

A prolonged whine-like call of variable volume.

Circling

The cock walks round a hen with exaggeratedly high steps watching her all the time.

The Rear Approach

This is the term given to the approach of the cock from behind the hen. Sometimes the cock will grab her comb or neck with his bill or he will stand over her and flap his wings vigorously.

Nine actions were found to occupy most of the observation periods and were performed by all the cocks. They were waltzing, tidbitting, wing-flapping, cornering, feather-ruffling, tail-wagging, head-shaking, bill-wiping and preening. The means of the relative frequencies of these actions for the summer and autumn are given in Table I. Also included but added together are the frequencies of circling, rear approach, placing of the cock's foot on the hen's back, and grabbing at the hen with a peck-like movement. As stated earlier, all these frequencies were obtained over the last third of each phase of the experiment. This method of sampling is assumed to reflect the courtship of the males fairly accurately, for the ranking of the cock for waltzing is identical for the sampling periods and the part of the experiment when waltz records were kept. The sex call was superimposed over most of these actions at various times by all the cocks but no record of its duration was kept.

Three of the actions, pre-copulatory waltzing, tidbitting and wing-flapping were analysed statistically, but the analysis was not applied to the other actions, as the numbers were small. In both seasons significant differences were found between the cocks for waltzing, tidibtting and wing-flapping.

Cock D waltzed significantly more than the other cocks in both seasons. In the summer data the other four cocks did not differ significantly in the number of times they waltzed, and in the same period the older cocks (A and B) generally tidbitted less and wing-flapped more than the younger cocks. In autumn tidbitting, wing-flapping and strutting were generally suppressed, but cornering increased. The cocks dust-bathed a great deal during this period and spent some time feeding. The greatest changes were found in A and E, but again the four cocks did not differ significantly in their rates of waltzing or generally approaching the hens. Bill-wiping was omitted in the autumn counts as most of the cocks fed while in the pens, whereas in summer bill-wiping had occurred without feeding.

So far only the actions easily scored have been discussed, but there were a small number of additional actions. A and B rarely chased the hens, whereas the younger cocks did so very frequently. D sometimes "screamed," which sounded like a shrill human sneeze. None of the other cocks in this experiment ever "screamed," but another cock was heard doing it. Strutting was often done by the younger cocks in summer, but only seldom by the older cocks; in autumn, however, it was generally suppressed. All these actions discussed above have been witnessed in pens where cocks have been with hens continually, so that they cannot be considered as aberrant by-products of the experimental procedure.

TABLE I. The Mean Number of Times Each Action was Performed by Each Cock in the Two Periods. Bill-wiping was Omitted in Autumn (See Text).

Actions	Pens	Summer					Autumn				
		COCKS					COCKS				
		A	B	D	E	F	A	B	D	E	F
Waltzing	11	3.6	4.2	20.5	8.0	11.0	1.5	2.0	19.5	1.5	9.0
	12	3.5	14.0	16.7	9.0	6.5	4.0	6.5	21.0	6.5	5.0
	13	4.3	4.5	18.5	8.0	6.0					
Tidbitting	11	5.0	5.8	35.0	5.6	11.0	12.0	1.5	28.5	7.0	10.5
	12	1.0	1.0	31.5	49.5	46.5	22.0	1.0	31.0	14.0	10.5
	13	9.3	1.0	32.5	26.0	*					
Wing-flapping	11	74.6	67.6	47.0	65.5	70.0	2.0	5.0	14.5	3.0	19.5
	12	60.5	83.0	55.5	32.5	60.5	3.0	5.5	14.0	3.5	10.5
	13	71.6	72.5	47.5	43.0	61.0					
Cornering	11	1.0	1.8	0.0	0.0	1.0	0.0	6.5	1.0	0.0	8.5
	12	0.5	0.0	0.5	0.0	0.5	0.0	2.5	0.0	0.5	2.5
	13	1.6	0.5	0.0	0.0	0.5					
Feather Ruffling	11	1.3	1.6	2.0	2.0	1.0	1.0	0.5	1.0	1.0	0.5
	12	1.5	2.0	1.5	0.5	1.0	0.0	0.5	0.5	1.5	1.5
	13	2.0	2.0	2.0	2.0	1.0					
Tail-Wagging	11	4.0	2.0	1.5	1.0	1.0	1.0	0.5	0.0	0.0	0.0
	12	3.0	1.0	2.0	2.5	4.5	1.0	0.5	0.0	0.5	0.0
	13	4.3	2.5	1.5	1.0	3.0					
Head-Shaking	11	0.5	0.8	1.0	11.5	2.0	13.5	1.5	2.5	13.0	3.0
	12	1.0	1.0	1.5	35.0	4.0	2.0	0.5	5.0	9.0	2.5
	13	2.0	0.5	1.0	22.0	2.5					
Bill-Wiping	11	4.0	1.0	1.0	1.5	2.0					
	12	1.5	1.0	0.6	1.0	0.0					
	13	3.0	0.5	0.0	4.0	0.0					
Preening	11	1.6	0.0	0.5	0.0	1.0	0.0	0.5	1.5	0.0	0.0
	12	1.0	0.0	0.5	0.0	0.0	0.0	3.5	2.0	1.0	0.0
	13	0.3	4.5	0.5	0.0	0.0					
Circling, etc.	11	1.6	1.4	1.0	0.0	4.0	1.0	2.0	0.0	0.0	1.0
	12	3.5	4.0	1.0	2.0	0.5	1.0	0.5	2.0	1.0	2.0
	13	5.6	3.5	0.5	0.0	0.0					

*Only one accurate reading was obtained for tidbitting by F in Pen 3 so it was omitted.

Male Behaviour and the Female Crouch

A non-significant correlation was found between the number of waltzes in an observation period and the number of crouches in that period ($r=0.23$, $P > 0.1$). The data from all the cocks in the sampling periods in both seasons was used for this calculation. As would be expected in a situation where so many variables may play a part, this result indicates that the relationship between waltzing and crouching is subtle rather than directly linear. It was decided that the sum of the frequencies of the apparently stimulatory actions might be a better yardstick of the courting of the male. Movements, to which the hens responded by advancing to the cock, or crouching to him, or avoiding him, were chosen. They were waltzing, circling, the rear-approach, and the placing of the cock's foot on the hen's back, tidbitting, cornering, and wing-flapping. The last three were chosen because hens had been seen to respond to them. When a cock tidbitted, the hens usually ran to him, and when he cornered they invariably ran to him. Wing-flapping mostly produced no overt response, but occasionally a hen crouched when a cock wing-flapped over her. The correlation coefficient was again non-significant ($r=0.24$, $P > 0.1$). Again, this result is to be

expected, for the actions used in this calculation probably need special weighting, and are unlikely to be of equal importance to the hens. Furthermore, taken out of their contexts, some actions may lose their value, which may depend upon complex relationships. Nevertheless, if a direct linear relationship existed this calculation would have revealed it.

Over longer periods, it was found that the cocks received different numbers of crouches from the hens. A chi square test was applied to the data from each pen for each season giving a total of 5 chi square values. The expected number of crouches received by each cock was worked out on the following basis. The time spent by any cock in a pen forms a proportion of the total spent by all the cocks in the pen, allowances being made for the absence of any hens, and if the total number of crouches is evenly distributed amongst the cocks, each would be expected to receive a number consonant with the fraction of the total time he spent in that pen. The rate of crouching did not decrease in autumn despite the fact that most of the hens were losing feathers. In summer a total of 267 crouches was recorded and in the autumn 287 was recorded. Significant chi square values were obtained for Pen 12 in the summer data ($X^2=11.62$ for 4 degrees of freedom), and for the same pen in autumn ($X^2=9.62$ for 4 degrees of freedom). In the autumn data the total X^2 for the two pens was significant at the 5 per cent. level ($X^2=15.77$ for 8 degrees of freedom), while the heterogeneity chi square was insignificant ($X^2=2.97$ for 4 degrees of freedom). The total chi square for the summer data was $X^2=19.19$ ($0.05<P<0.1$) and the heterogeneity chi square was $X^2=12.6$ for 8 degrees of freedom. $P>.05$.

In order to distinguish which of the cocks was responsible for these high chi square values, the deviations between actual and expected values for each cock as shown in Table II, were subjected to analysis of variance, and it was found that the cocks differed significantly at the 5 per cent. level ($F=3.31$, df 4 and 15). The error term allows the least significant differences between mean deviations to be calculated. On this basis any difference of more than 7.1 between two means is significant. Thus the cock D differs from the cocks A and F and the difference between A and B tends towards significance.

In comparing these cocks another question remains: did all the hens respond similarly to the cocks? It is quite possible that a few highly sexually active hens turned the number of crouches in favour of cock D. Nine of the 15 hens in pens 11 and 12 crouched to the cocks D and A at sufficiently high rates for their data to be analysed statistically. The results are given in Table III. The total chi square and the non-significant heterogeneity chi square show that there was a general tendency amongst the hens to favour cock D. However, two of the

TABLE II. The Deviations between the Actual Number and the Expected Number of Crouches for Each Cock in Each Pen for the Two Seasons

	Cocks				
	A	B	D	E	F
Deviation Pen 11	—1.5	+0.1	—0.2	—2.1	+3.7
Deviation Pen 12	—6.9	—0.4	+9.8	+5.1	—7.4
Deviation Pen 13	+2.2	—0.4	+6.8	—5.7	—2.8
Deviation Pen 11	—12.0	+1.1	+3.4	+3.7	+4.1
Deviation Pen 12	—11.4	+3.5	+10.7	—0.5	—2.3
Mean Deviation	—5.9	+0.8	+6.1	+0.1	—0.9

Least Significant Difference = 7.1

individual chi squares were significant, indicating that some hens were very much more affected than others. Similarly, in the 6 hens whose data were not analysed statistically there was a general tendency in favour of D, whilst in two hens this was very marked indeed. These four hens which crouched a great deal to cock D had very different rankings as far as sexual activity was concerned. Therefore, it does not seem to be merely a case of the more active cock obtaining a greater response from the less sexually active hens or the hens with a high sex ranking.

An examination of the data in Table II shows that the difference between cocks D and F stems mainly from the performances in Pen 12, and the data of individual hens in Pens 11 and 12 confirms this. In Pen 11 no general tendency to favour either cock was found and although none of the chi square values were significant, 5 out of the 8 hens crouched more to F than to D. In Pen 12 the data of 5 of the 7 hens were large enough to be treated statistically. These hens all crouched more to D than to F, although only in the case of one hen was the difference significant. These results are shown in Table IV. A comparison of this sort between cock A and B was not feasible, as there were data for only a few hens that could be analysed statistically.

It was stated earlier that the difference between D and F is due mainly to their performances in Pen 12. An examination of Table I shows that F behaved rather differently in the two pens and was generally vigorous in Pen 12 than in Pen 11. He waltzed, wing-flapped, and cornered less, and in the summer circled a good deal less in Pen 12 than in Pen 11. This supports the contention that D due to his assertive courtship, received more crouches, while A, who was more passive, received less than expected.

Table III The Actual and Expected Number of Crouches given to the Cocks A and D by 9 Hens from Pens 11 and 12 in Summer and Autumn

Hen	Crouches		Chi Square
	Cock A	Cock D	
3607	Actual 3 Expected 5.5	8 5.5	1.45
9348	Actual 0 Expected 5.3	11 5.7	8.34*
9359	Actual 4 Expected 6	9 7	0.69
7993	Actual 16 Expected 11.9	12 16.1	1.89
3232	Actual 4 Expected 5.5	9 7.5	0.31
2000	Actual 6 Expected 7.7	9 7.3	0.37
3067	Actual 10 Expected 15.6	25 19.4	3.00
9358	Actual 3 Expected 8.5	15 9.5	5.50*
2111	Actual 7 Expected 8	6 5	0.08
	Total chi square Heterogeneity chi square	9 d.f. = 21.63* 8 d.f. = 9.94	

* Indicates significant chi square values at the 5 per cent. level.

TABLE IV. The Actual and Expected Number of Crouches given to the Cocks F and D by Five Hens from Pen 12 in Summer and Autumn

Hen	Crouches		Chi square
	Cock D	Cock F	
2000	Actual 9 Expected 6.2	2 4.8	1.95
3621	Actual 9 Expected 6.3	4 6.7	1.3
3067	Actual 25 Expected 16.3	7 15.7	8.4*
2111	Actual 6 Expected 5.7	5 5.3	0.03
9358	Actual 15 Expected 13.5	12 13.5	0.15
	Total chi square (5 d.f.) = 11.83* Heterogeneity chi square (4 d.f.) = 1.73		

* Indicates significant chi square values at the 5 per cent. level.

Discussion

The five cocks examined here were found to differ in the frequencies at which they performed certain actions in the presence of hens. A low and non-significant correlation was found between the number of waltzes performed in an observation period and the number of crouches received during that period. Furthermore, when the frequencies of the actions that elicited overt responses from the hens were added together, and tested with the number of crouches elicited in the same observation period, the correlation coefficient was again found to be low and non-significant. This was taken to mean that these actions probably have a partial and indirect effect on the rate at which the hens crouch. Over the entire period of the experiment, however, it was found that the cock D received significantly more crouches than the cocks A and F, while the difference between A and B tended towards significance.

D waltzed significantly more than the other 4 cocks in both seasons. He tidbitted at a consistently high frequency and generally courted in a forceful manner, chasing the hens, often strutting, and occasionally "screaming." His vigorous courting may account for his generally receiving more voluntary crouches than would be expected. The cock A waltzed less than the other cocks and this may account for discrimination against him. This supposition, however, seems unlikely. In the summer data from Pen 11 the negative deviation between his expected number of crouches and his actual number of crouches is less than that of E, who waltzed more. In Pen 12 for the summer it is less than that of F who waltzed more. In the autumn data from Pen 11, he waltzed more at the same rate as E and at nearly the same rate as B, but his deviation was far larger than theirs in a negative direction. In Pen 12 he waltzed at only a slightly lower rate than F but again received many less crouches. These considerations show that waltzing alone does not appear to be all important, a fact shown by the low correlation coefficient mentioned earlier. It is most probable that the difference between the number of crouches received by D and A may be due to overall differences in their behaviour, for it must be remembered that the methods employed here, both experimental and statistical, are crude and subjective, and that some actions really require special weighting in order that they may have their true biological importance. Nevertheless, it seems unlikely that waltzing alone can account for the difference in the number of crouches received by the cocks D and A. By further statistical analysis, the relationship between a male action and the female crouch may be examined in more detail, and such work is to be undertaken.

The Courtship of the cock includes apparently aggressive movements and also possibly fleeing movements. In this study the younger cocks,

particularly in the summer, were very much more forceful in their courting than the older cocks (A and B). They chased the hens and displayed more by waltzing and strutting than the older cocks whose main form of display appears to have been wing-flapping, which does not have the same overt effect on the hens as other displays. Generally the younger cocks tidbitted more and it was accompanied by displays indicating that it found an outlet for an excess of sexual energy when the drive could not find consummation. In the autumn, cock A tidbitted a great deal, but as he displayed at very low frequencies this displacement reaction was probably due to a low sex drive in conflict with another drive. All the cocks were moulting in autumn and display was generally reduced. Feeding in the pens increased, indicating less sexual activity. Dustbathing occupied much of the time, and although this may be a displacement reaction, it is suggested that while the cocks were moulting it may often have been done for physical reasons.

To return to differences between individual cocks, it is easy, when comparing D and A, which form two extremes, to account for D's success by his more vigorous display; but when the intermediate cocks are considered the picture is less clear cut. As far as display is concerned B ranks fourth, for he waltzed little and never strutted or chased the hens, yet he received more crouches than E and F. He was slightly larger than the other cocks, and this factor may have been important. It seems unlikely, therefore, that differences in courtship behaviour are entirely decisive in determining a cock's success, although it is a very important factor.

Summary

The mating behaviour of five Brown Leghorn cocks was analysed in detail, and the number of voluntary crouches accorded them by three pens of hens were recorded. Nine actions were found to be performed by all the cocks, at frequencies fairly characteristic for each cock. They were waltzing, "*tidbitting*," wing-flapping, cornering, feather-ruffling, tail-wagging, head-shaking, bill-wiping and preening. The most active and forceful cock received the greatest number of crouches, and the less active cock, the least number of crouches. All the birds showed a tendency to favour the more vigorous cock, but some were significantly more biased than others. A third cock received less crouches than the alpha cock in one pen, but not in the others. The effect of waltzing on the rate of crouching is discussed and from the present data is not assumed to be all-important. Furthermore, the ranking of the cocks with regard to the number of crouches received cannot be accounted for entirely in terms of behavioural differences.

A qualitative interpretation of the cocks' actions suggests that pre-copulatory waltzing, which is also found in cock fights, is a threat display, but that post-copulatory waltzing may be a "displacement reaction."

Wing-flapping is also probably a display movement. Tidbitting and cornering are "displacement reactions" that may aid the cock in his courtship. Feather-ruffling, preening, bill-wiping, tail-wagging and head-shaking are also considered to be displacement reactions.

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The Spawning Behaviour of Brown Trout and Salmon

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I. Introduction

Jones & King (1949), by using special facilities and equipment for observation, were able extensively to supplement, and in some respects to correct, previous accounts of the behaviour of spawning salmon. Field observations of fish under strictly natural conditions are extremely difficult to make and to interpret, so, although a number of descriptions have been published of the behaviour of brown trout on their spawning beds in the river and in tanks it seemed possible that the experience gained in the salmon work would serve to amplify the results of previous studies. This expectation has been more than fulfilled. Not only has it been possible by using observation tanks to describe and classify many varieties of behaviour of which interpretation in the field must always have remained doubtful, but it has been found that the central event of the whole pattern, the orgasm, is completed so quickly in this species as to make adequate description impossible without the aid of slow-motion cinephotography.

The fish in the tanks were subjected to unnatural conditions in that they were unable to leave the tanks which were illuminated almost continuously. Most of the physical changes that take place in the river (e.g. temperature and turbidity of the water) were reflected in the salmon tank. In the trout tank, in addition, the water was recirculated and the water temperature was fairly constant (10° to 13°C, generally 10 to 11°C). Over the seven successive spawning seasons when the salmon were under observation for approximately three thousand hours, over eighty orgasms were seen and filmed by one of us (J.W.J.). Thirteen trout orgasms were seen and filmed. Despite the unnatural conditions to which the fish had been subjected there was little variation in the behaviour of the fish at any one spawning; it is felt therefore that the spawning acts as seen in the tanks can be regarded as normal.

Day (1887) gives no account of the spawning habits of brown trout but describes the spawning of salmon and suggests that the process is similar in all Salmonidae. Greeley (1932) observed one spawning of brown trout; he describes the 'courting' by the male, the cutting of the bed by the female, the simultaneous orgasm in both sexes and the covering up of the eggs by the female. Hobbs (1937) gives a somewhat fragmentary description; he interprets a typical male 'courting' quiver as being the male orgasm, and infers that the female deposited eggs at or about this time. Curtis (1949) gives an account of the spawning of the steelhead trout and states that it is essentially similar in the brown trout. Stuart (1953) observed trout spawning on gravel beds in the river. He considers that the male shows definite territorial behaviour, and describes an 'intimidating display achieved by a peculiar distension of the opercular plates with the mouth wide open, accompanied by a rigid flexion of the body to form a shallow arc, the head and tail pointing towards the intruder.' In captive trout Stuart observed that in this display each fin was maximally extended and the body quivered with tension. This last observation suggests that Stuart is here referring to the common quiver (see below).

There are several descriptions of the spawning behaviour of other Salmonids: Hazzard (1932) on the Eastern Brook Trout (*Salvelinus fontinalis* Mitchell), Royce (1951) on American Lake Trout (*Cristivomer namaycush*), van Someren (1953) on Rainbow Trout (a form of *Salmo gairdneri* Richardson), Briggs (1953) Silver Salmon (*Onchorhynchus kisutch* Walbaum), King Salmon (*Onchorhynchus tschawytscha* Walbaum) and Steelhead Trout (*Salmo gairdneri* Richardson). Fabricius (1953) has given a detailed analytical account of the spawning behaviour of the Char (*Salmo alpinus* Linn.) as seen in an aquarium tank. Jones & King (1949 etc.) give a full description of the spawning behaviour of the Atlantic Salmon (*Salmo salar* Linn.) and a review of previous work on this species.

II. Material

On October 27th, 1953, several fish were caught by electric fishing in Afon Lliw, which

* Work being carried out with D.S.I.R. grant.

runs into Llyn Tegid (Merioneth). Some of these were three-year-old fish which were ripe. After being kept in well-aerated water in the laboratory, some of the fish were transferred to the observation tank. A pair of these fish spawned at 1.00 a.m. on November 12th. Owing to an accident to the pump during the night of November 14/15 most of these fish were lost, and because of floods it was not possible to capture more fish in the Lliw and other rivers. On November 18th six ripe females and four ripe males, all three years old and about 11 inches in length, were purchased from Chirk Fish Hatchery.

III. The Obervation Tank

The tank was 72 inches long, 16 inches deep, and 13 inches wide: its floor and back were of metal sheet and the front was covered with $\frac{3}{8}$-inch plate glass (Fig. 1).

A slot sluice opened into the top end of the observation tank from a reservoir tank whose sides were each approximately sixteen inches long. At the outflow end of the observation tank a controllable sluice opened on to a sloping surface which led into a second reservoir tank of approximately the same size as the first. From this tank a two-inch pipe led to the pump, and from the pump into the inflow reservoir tank.

The floor of the observation tank was covered with a layer of six to eight inches of unwashed gravel from the shores of Llyn Tegid. This gravel varied in size from a quarter of an inch to two inches and was mixed with a considerable amount of coarse silt.

About fifty gallons of water a minute was circulated by the centrifugal pump; this was supplemented with about four gallons a minute of mains' tap water. An overflow pipe carried the excess water from the outflow reservoir tank.

Under working conditions the depth of water in the tank ranged from two and a half to four inches. When the water was two and a half inches deep the surface velocity was twelve inches a second, and it was about half as fast when the water was four inches deep. In each case the velocity at an inch below the surface was about the same as at the surface.

IV. Definition of Terms Used

Bed. One depression made in the gravel by the female.

Crouch. The position adopted by the female in the later stages of feeling the bed.

Cutting. The making of the depression or bed in the gravel by the female.

False Orgasm. An incomplete orgasm in which the female crouches in the bed, opens

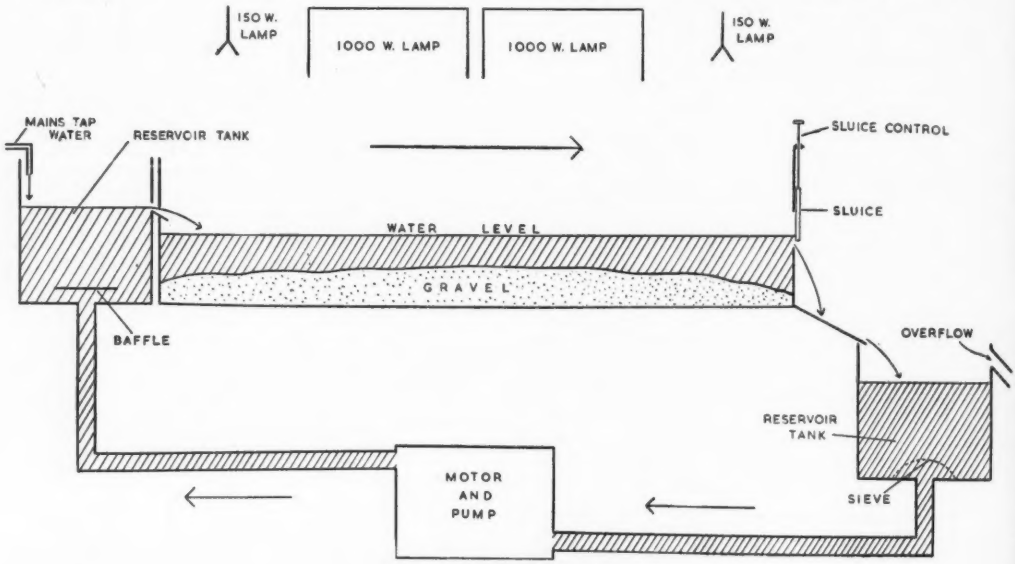
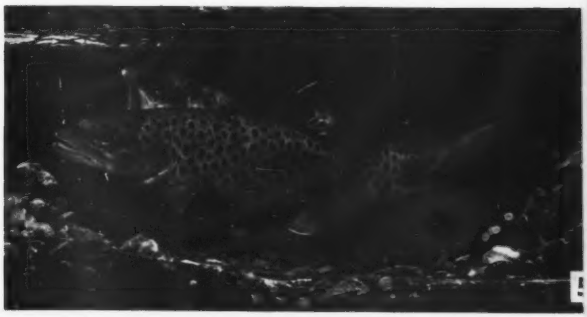
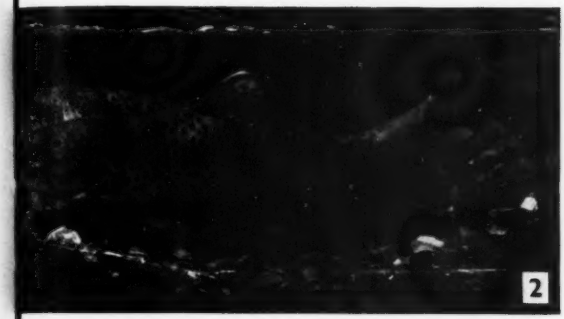


Fig. 1. The observation tank

PLATE I





1. A female 'cutting'
2. Quivering (courting) by the male (nearer the glass). The female was crouching on the bed as the male moved alongside: as he quivered she rose from the bed.
3. Feeling or testing the bed by the female. Here the female has just backed into the bed, stopped herself with her caudal fin, and is about to 'crouch' into the bed.
4. Fight. Here the tenant male is attacking an intruding male.
5. An Orgasm. The female is crouched, fully tensed with wide open mouth; she has started passing out eggs, some of which can be seen bouncing up from the bottom of the bed. (This loss of eggs is rare). The male has finished his ejaculation and has almost closed his mouth.
6. Covering up. A female moving upstream immediately after an orgasm disturbs some of her own eggs. The male stands by.
7. A male stands by as the female covers up her eggs.

THE SPAWNING OF BROWN TROUT

PLATE II

Fig. 1. A TROUT REDD

First view of eggs. After removing about two inches of gravel the two large stones seen on the right are exposed: removal of these exposed about twenty-five eggs.

Fig. 2. A TROUT REDD

More eggs are exposed as fine gravel is removed.

her mouth as if to spawn but does not do so. Meanwhile, she is joined by the male who opens his mouth, quivers, and sometimes passes out some sperm before the female relinquishes the crouch position.

Feeling. The testing of the gravel by the female with her anal fin and sometimes also with her pelvic fins.

Orgasm. The actual and almost simultaneous extrusion into a bed of a quantity of eggs by the female, and of sperm by the male.

Redd. Gravel in which eggs have been laid.

Spawning Act. The sequence of events starting with the first cut by the female, including one orgasm and ending with the covern up of the eggs.

V. The Typical Sequence of Events in One Spawning Act

1. The female explores the gravel and carries out exploratory cutting.
2. Some of the males fight. One male assumes dominance and quivers against the female.
3. The female concentrates on cutting in one place. The dominant male continues to quiver against her and repels any other males, or females, which try to intrude. The female tests her bed by means of her anal fin and, sometimes, her pelvic fins.
4. When the female trout has made a bed about three inches deep she crouches into it (six or more inches in salmon). The male darts forward alongside her and quivers: eggs and sperm are extruded almost simultaneously as the fish lie in the bed with their mouths open.
5. Immediately afterwards the female moves upstream and by rapid cutting sends down gravel to cover up her eggs; subsequently she starts preparing her next bed.
6. The whole process may be repeated several times. The principal events in this sequence are illustrated in Plate I, 1 to 7 (inc.).

VI. Various Aspects of the Spawning Behaviour

Except where stated the following section applies to both trout and salmon.

A. The Quiver

It is possible to distinguish five different circumstances in which the male trout and salmon has been observed to quiver. In each case the body movements are similar and take the form of a short sequence of rapid quivers or shudders in which the whole body is involved and at the same time the dorsal, pectoral and pelvic fins are erected. Sometimes the quiver is accompanied by mouth opening and slight distention of the opercular plates. There is little difference in the quivering of salmon and trout (Plate I, 2).

(*a*) When the male quivers in close proximity to a female either when she is cutting or feeling the bed, such activity is usually preceded by a dart forward, which takes him to a position alongside the female, usually so that his head lies in line with the posterior end of her pectoral fins. Quivering starts before the end of the forward movement, and continues as he lies alongside the female: the female then moves away and the male retires. The forward dart may start at an angle to the body of the female, but it usually ends with the bodies of the fish parallel to each other. This quivering increases in intensity and in frequency of occurrence up to the orgasm. Only rarely does a male attack the female by biting after a bout of this quivering activity. Fabricus (1953) describes how char when quivering open their mouths, especially in 'high intensity courting acts.' This gaping rarely occurs in salmon and trout other than at the orgasm.

(*b*) The male may quiver, in a manner indistinguishable from that described above, against a female who is resting in the bed and has been inactive for some time: but, in this case, unless the female responds by a resumption of cutting after two or three quivers, the male sometimes attacks her by biting.

(*c*) The male may also quiver at some distance away from the female. Male salmon and trout have been observed to quiver respectively at approximately three feet, and one-and-a-half feet downstream from their respective females. Again, the body movements in the male appear to be identical with the quiver given in proximity to the female, but are not preceded by the preliminary dart.

(*d*) Males also often quiver alongside intruding males and occasionally against males lying passively some distance from the bed. Fighting results if the intruding males fail to respond by moving away either from the female or the bed.

(*e*) The quiver of the male during the orgasm is again a similar sort of body movement except that in this instance the male lies in the bed alongside the female with his head in line with hers.

Female trout have been seen to quiver in

almost the same way as the male trout and salmon, but possibly with less movement of the head. The female quiver is rare and was seen on three occasions only, twice against other females and once against a male. Both the females that quivered were normal and spawned later. Quivering by female salmon has not been observed.

Just before the orgasm the female trout makes a movement which is very like a quiver, but it consists of rapid lateral movements of only the posterior half of the body. It seems to be a exploratory movement, or an attempt by the female to clear, with her anal fin, the region where the eggs will lie.

B. Fighting

The fish, especially the trout, fight viciously. Most of the fighting is done by the dominant male who attacks all intruding males and females. Biting is common, and this often follows a lunge with open mouth and distended gill covers; the region most often attacked is the tail and wrist, and sometimes the back, snout and pectoral fins. The smaller fish are sometimes held in the mouth and shaken for several seconds. The dominant male is in turn sometimes bitten by the cutting female, but never by the subordinate males though they may make tentative snaps at his tail. Whilst the female is cutting the dominant male lies just behind her and the subordinate males, when interested, lie in line astern from him. When this happens each male seems to dominate the male immediately behind him. On one occasion a line of five male trout approximately in order of decreasing size attended the female: at intervals a movement forward by any one of the four posterior males started a bout of snapping and biting initiated by the fish immediately ahead of the fish which moved forward.

Male dominance is, however, not always immediately determined by size. On one occasion a male trout two inches shorter than an intruding male retained his dominance during a fight and for some time afterwards. He was driven off by the intruder just before the orgasm; nevertheless he returned to the bed during the orgasm and ejaculated. This was the only instance where two males were seen to spawn at the same time with one female

Formal Fighting in Trout

In addition to the short bouts of snapping and chasing described above, three prolonged fights between trout of about the same size were witnessed each lasting about ten minutes. These prolonged fights follow distinct patterns and will be called formal fights. They have been seen only when the participants are roughly the same size; fights between fish of markedly differing

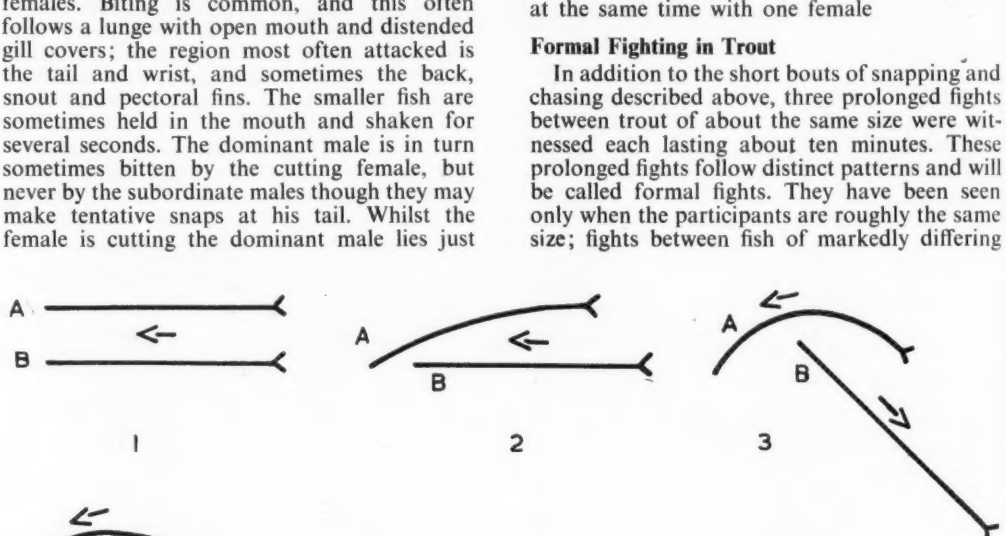


Fig. 2. Formal fighting between two female trout.

size are short and in each encounter the issue is decided before there is any opportunity for the formal pattern to become evident.

(i) **A formal fight between two females.** This was a fight between two females which were preparing beds at different places in the tank. In this fight, the pattern of fighting was based on a feature characteristic of female behaviour: a female preparing a bed will not allow another fish to lie ahead of her. If an intruding fish (of either sex), approaching from behind, moves past the female in the bed and comes to rest with its snout an inch or two ahead of hers, she moves forward until the snout of the intruder is just behind the level of her eye. The movement ahead of the intruder is termed the 'challenge' and the resulting movement of the tenant is called the 'position-adjustment.' In the fight, repetition of these two moves resulted in a 'parallel forward progression' in which the opponents moved slowly upstream pausing slightly between each position adjustment and the next challenge. The forward progression was interrupted when the challenging fish (A), in moving forward, cut in across the path of the other (B), (see fig. 2). The rear fish (B) after backing an inch or two then launched herself bodily on to the flanks of the challenger (A) with fins erect and mouth wide open. As a result the challenger immediately twisted around in a complete circle, generally avoiding contact with the mouth of the attacker and the two fish once more came to lie side by side, as will be seen from fig. 2.

Movements (4) and (5) were very rapid and caused much water disturbance. The distance covered whilst movements 1-6 were carried out was only slightly more than the length of the fishes (11 inches). The fish then resumed the parallel forward progression, interspersed with further flanking attacks, these becoming more frequent and vigorous. The climax was reached just as the fish approached the upstream limit of the tank. Here (B), which was the rear fish at this moment, fastened her mouth tightly on the base of the lower lobe of the caudal fin of (A), and then backed downstream dragging (A) slowly but strongly backwards. At intervals of about two seconds she shook (A) violently. The latter appeared to make no efforts to escape, until she finally wrenched herself free, after being dragged backwards a distance of over five feet. Female (A) then darted upstream, and (B) followed after a pause. There followed more 'parallel forward progression' but the fighting was less orderly than before. Finally fish (B) retired to the pool at the downstream end of the tank. The outcome of the fight was obscure. Fish (A) never spawned despite the fact that she was the dominant female for the next 53 hours. Then (B) came up from the pool, cut a bed 4 feet behind (A) and spawned 2 hours later.

Several instances of parallel forward progression of shorter duration were observed. The 'challenge' is sometimes given by the tenant, and in parallel forward progression first one fish then the other may make the 'challenge' movement.

ii. **Formal fighting between males.** This fighting takes place just before one male has assumed dominance, and dominance may be determined as the result of such a fight. Male tactics were very different from those of the females. A challenging male moving up from the downstream end of the tank would stop about 9 inches away from the tail of the other fish and both fish often dropped downstream slowly about nine inches apart with their long axes about 45° to the current, or they often lay facing upstream, one about a foot behind the other. The actual attack varied: frequently the upstream fish, in one rapid movement, turned and darted at the other with mouth wide open and fins erect, often fastening his mouth on the flanks or snout of the opponent (see Plate I, 4). Sometimes the downstream fish darted at the other with mouth wide open and fins erect. Occasionally the rear fish swam slowly forward in front of the other who often replied with a quick snap at the moving tail ahead. In each case the attack was a quick dart with open mouth and slightly distended gill covers up to the opponent ending with the mouth grasping some part of the others' body (Plate I, 4) The fish so attacked did not at first swim away; he usually wrenched himself free, and the fish resumed their fighting positions or postures. In each fight the winner was the fish whose attacks had been the more vigorous and frequent. In one fight, when the water in the tank was about 9 inches deep, the fish which eventually won always postured at about 45° to the horizontal with head high and tail touching the gravel. This may be a 'dominance' posture. Sometimes during these male fights another pattern of shorter duration was observed: the two fish swam in a circle each trying to grab the other's tail, the pattern being

broken when one fish swam away followed by the other.

Greeley (Belding, 1934) witnessed two or three fights between rainbow-trout males on their spawning grounds. Describing them he says: 'They may then leave the nest, swim upstream side by side, and then one of them will drop downstream, get a good run and strike the other just as hard as he can amidships. The male attacked will accept that bite without any display of fear and will in turn drop downstream to get a good run and attack the other fish in exactly the same way. I have seen two big rainbows evenly-matched, twenty-seven to thirty inches long go downstream . . . and attack each other in that way.'

It is clear from this that the type of male fighting observed in the tank is a normal occurrence amongst rainbow trout in the natural stream, and that Greeley saw a normal male trout type of attack.

There is probably less actual biting in the fighting of salmon, though males have been observed dragging females backwards. Formal fighting is very much as in the trout.

Two other activities whereby fish of either sex drive away intruders have been mentioned previously (Jones & King, 1952); they seem to be related to fighting.

(i) When an intruder enters the bed, the tenant male or female moves a short distance ahead and drops back, tail first, towards the bed. A few inches ahead of the intruder's tail the tail is flicked laterally in a way which, though easily recognized, is very difficult to describe. The withdrawal downstream of the intruder is an invariable consequence. This behaviour is termed 'tail-flicking.'

(ii) When an intruder moves into the bed the tenant fish (of either sex) will move upstream so that the middle of its body lies slightly ahead and at an angle to the snout of the intruder. The intruding fish usually gives way by dropping downstream slowly, and the fish move downstream in this position. The intruder after a short time invariably swims away.

C. Preparation of the Bed by the Female

In both salmon and trout the genital papilla of females cutting a bed protrudes through the vent and appears to increase in size as excavating continues. The papilla of an 11-inch trout may protrude an eighth of an inch.

Whilst preparing the bed the female displays two types of movement, cutting and feeling. Cutting is concerned with the displacement of gravel and feeling is the process by which the female tests the results of her cutting activities.

To carry out the process of cutting the female turns over on her side and by alternately bending and straightening her body produces a vigorous vertical flapping of her tail as a result of which gravel immediately beneath the spread caudal fin is dislodged as the fin moves upward and forward quickly. Slow-motion cinephotography revealed that the description of the salmon cutting activity given by Jones & King (1950a) applies also in detail to the cutting process in the brown trout, i.e., 'The film shows that in her cutting movements the female starts from her normal position, i.e., with head upstream, body on an even keel, and almost parallel to the bed of the river. She then turns over on her side by firstly rotating her caudal fin so that it rests almost flat on or near the gravel and follows this by a lesser rotation of the rest of her body which in this phase has its dorso-ventral axis at about 45° to the bed of the river. A bending of the body follows. In this phase the posterior half of the body is bent sharply downwards and the caudal fin rests fanned out on or near the gravel. The bending of the anterior part of the body is less pronounced, so that the head is often only slightly lower than the middle of the body.' (See Plate I, 1).

'From this position rapid straightening (the upstroke) and bending (the downstroke) of the body follow so that the posterior region of the body is thrust vigorously upwards and downwards from and to the gravel. This complete action of flexing and straightening the body occurs several times in rapid succession and in the more vigorous cutting movements the anterior part of the body may be more bent. Throughout these movements the pectoral, pelvic and dorsal fins are erect and the mouth is open slightly.

'It is suggested that the vigorous downstroke of the posterior half of the body thrusts the water against the gravel with sufficient force to loosen it, and that the upward flexion further assists the movement downstream of the displaced gravel by an upward suction.' There is now no doubt that it is the suction produced by the upward movement of the fanned caudal fin that is the cause of the movement downstream of the gravel in the cutting action.

The complete action of flexing and straightening of the body is termed a cutting movement,

and a complete series of such movements beginning and ending with the fish in normal position is called a cut. A weak cut consists of only a few cutting movements and these are slow and languid. A strong cut may consist of as many as a dozen vigorous cutting movements in rapid succession at the rate of about three or four a second. After a cut the female usually feels the bed with her anal fin and sometimes also with her pelvic fins. (Plate I, 3).

A typical preparation of the bed by the salmon has been previously divided into two stages, (Jones & King, 1950a), i.e., early and late cutting. It is now felt that the process can be conveniently divided into four successive stages (for both salmon and trout), which are not rigidly distinct, though each is characterised by a particular type of cutting and feeling, and degree of attention by the male.

Stage I

Random cutting occurring shortly after the female has left the pool in which she has been lying in a her inactive period. Each cut consists of only a few weak cutting movements, and often the front part of the body is hardly rotated from its normal position. The males take little interest at this stage.

Stage II

Cutting still apparently exploratory, but the female tends to move more systematically upstream. The cuts are very long and vigorous, sometimes at an angle to the current. Feeling of the bed may take the form of backing slowly downstream with pelvic and anal fins touching the disturbed gravel: or she may turn and swim rapidly downstream with fins clear of the gravel back to where she started her cut, and here turn rapidly upstream again and move over the disturbed gravel with anal and pelvic fins trailing over it. The male is generally in attendance near the bed and quivers occasionally alongside the female in the intervals between cuts.

Stage III

This stage is reached when the exploratory cutting of Stage II has given place to cutting and feeling directed at a single limited area. The female has produced a sizeable depression in the gravel (about 2-3 inches deep). This depression is carefully felt as she backs over it or moves slowly sideways and forward with pelvic, and particularly the anal fins touching the gravel (Plate Ic). At this stage the backing and feeling may start at the bottom of the depression and be continued backwards over the downstream extremity of the bed. The male is usually very attentive, he quivers frequently, sometimes three or four times between every cut. Cutting at this stage still moves a fair amount of gravel.

Stage IV

The beginning of this stage is marked by a change in the type of feeling which can now be described as a 'slow bounce.' The female poises in the water with anal fin erect and drops down gently so that the fin touches the gravel. This is repeated after further cutting, and when the fin finds a crevice between two of the larger stones at the bottom of the bed, the sequence of bouncing and feeling appears to become less tentative and more purposeful: the erect anal fin is pushed hard down at the bottom of the bounce and as she rises it is moved sideways gently between the rocks. Often as the fin is pushed down the body assumes a curvature in which the head is elevated and the pelvic region fits snugly on the gravel. This position is defined above as the crouch. The crouch is retained for a second or two, and, if the bed is suitable, is followed by the mouth opening, the movement of the male into the bed, and orgasm. Cutting at this stage is less frequent and seems to be directed towards rearrangement of the stones at the bottom of the bed. The female now rarely moves out of the bed as she cuts, the tail

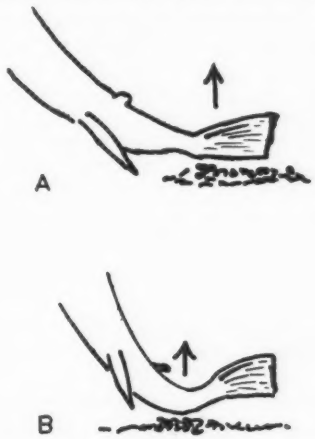


Fig. 3. A. Normal cutting technique
B. Stage IV variant.

being flapped several times over the same small area of gravel. Stage III cutting would carry her forward from the centre of the bed and would

send back gravel into the bed, and fill up the crevice which she requires between the larger stones. The female may at this stage vary her cutting technique: this change is shown diagrammatically in Fig. 3. In B the 'tail' is used instead of the tail fin.

It is thought that the female is not satisfied with her bed until she can crouch into the bed so that her anal fin is completely hidden between the two large stones in the bottom. Each time the female crouches the attendant male darts forward, lies alongside her, and quivers vigorously.

The above succession of stages is seen only when conditions are suitable, interruptions may stop cutting in stages I-III, but once stage IV is reached, cutting persists despite interruptions.

D. The Orgasm

The orgasm follows a crouch feel which has proved satisfactory to the female: she now remains in the bed and opens her mouth. The male joins her and quivers violently as he opens his mouth; the female then opens her mouth wider (to an angle of about 130°), raises her head and bends her body so that she appears to be in a state of extreme muscle tension as she passes out her eggs; (Plate I, 5). Most of the eggs pass down between the two large stones where the anal fin lies. The male raises his head, but not so much as the female and sperm is ejaculated under some pressure to the bottom of the bed as he quivers. The excess sperm appears a few moments later as a white cloud.

E. The Covering up of the Eggs

Immediately after ejaculation the female moves upstream and with vigorous cutting activity covers up the eggs. (Plate I, 6 and 7). At the end of each cut she often turns, and darts downstream to one side of the rear end of the bed and swims quickly along its rear edge; a quick turn then brings her back into the bed. The vigour of this operation suggests a defence against intruders.

A typical bed for a trout of about 11 inches in length takes the form of a saucer-shaped depression ten to twelve inches in length, three inches in depth to the top of the large gravel. The eggs are covered up in one or two minutes after deposition; the female then goes on to stage III cutting which will produce her next bed.

VII. Discussion

Tinbergen (1951) has described the reproductive behaviour of the three-spined stickle back and has postulated a hierarchical organization of drives underlying it. He adds that 'nearly nothing is known in detail about the way it works out in the various drives and in different species of animals.'

Our observations of salmon and trout can be represented as the expression of a similar hierarchy as shown in fig. 4.

The sequence of the reproductive pattern

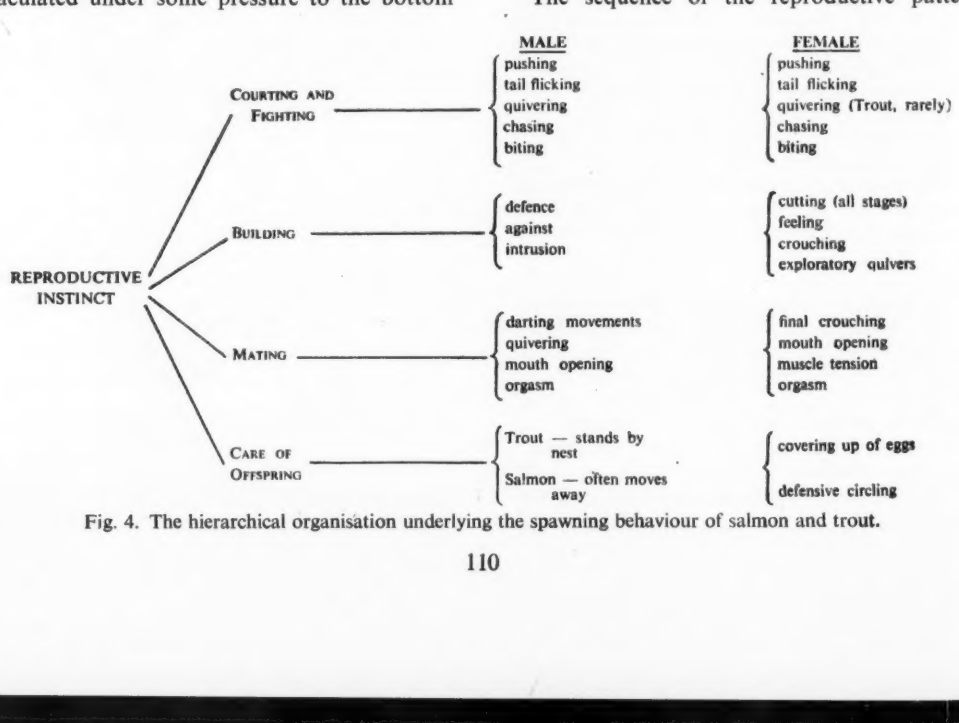


Fig. 4. The hierarchical organisation underlying the spawning behaviour of salmon and trout.

is dependent on sexual maturity: it is absent in immature fish. Male salmon in full spawning livery, but castrated by removal of testes, have been observed cutting a bed in the presence of ripe female; on the other hand male salmon, sterilized by ligature of the testicular duct continue to behave as normal males and go through all the stages of spawning without passing sperm (Jones & King, 1952). Gravid female salmon from which eggs could not be forcibly extruded by pressure on the flanks (showing that the eggs were not free in the body cavity) remained inactive in the observation tank despite the attention of the males. It is thus probable that in both salmon and trout females the primary activator which stimulates the start of the spawning pattern is the ovulation (or freeing of eggs from the ovaries into the body cavity). The attention of the male is necessary for the continuation of the pattern: female salmon and trout have been seen to start cutting in the absence of a male, but not to proceed beyond the first stage. Instances of a curtailment of the complete pattern have also been observed when female salmon which had spawned normally with adult males, ceased cutting on the removal of the adult male, and resumed on his return.

It is not yet possible to give an ethological analysis of this salmon and trout behaviour in such detail as that presented by Tinbergen (1951) for the three-spined stickleback. Further experimental work is necessary. Nevertheless it is worth while examining some aspects of the salmon and trout behaviour in the light of additions made by modern ethologists to our knowledge of innate behaviour.

1. The Male Quiver

The male quiver in both salmon and trout is used almost exclusively by the dominant male; other males even though fully ripe rarely quiver. At times when two females have been cutting beds in different parts of the tanks each has been attended by her own dominant male and in this case both males quiver.

As described above, the male quiver may take place alongside a female, at a distance from a female, against a male, or against a wall. In some instances a male quivered against a female, moved away and quivered against a male. It is not easy to classify the functions of these quivers, but they can be divided into three groups:

(i) Quivers not followed immediately by fighting.
(ii) Quivers followed by fighting.
(iii) Quivers ending in an orgasm.

(*a*) *Nature of the Quiver*

The importance of the male quiver, demonstrated by its frequent occurrence throughout the spawning act, warrants a discussion of its nature and function. The salmon quiver has been previously called 'courting behaviour' (Jones & King, 1949), and later compared with a displacement reaction (Jones & King, 1950a): further observations of this behaviour have shown that it cannot be regarded as a displacement reaction as described in other animals by Tinbergen (1952).

The 'courting' quiver is identical with the orgasm quiver, but sperm is not ejected. Tinbergen (1952), Fabricius (1953) and others have given examples of the isolated occurrence of activities which are parts of longer or more elaborate behaviour patterns: the full pattern does not appear either because the internal motivation of the drive is too low, and the various motor components the of pattern have different thresholds, or because the necessary sign stimuli are not present. It is probable that the 'courting' quiver of trout and salmon is in fact just such an isolated part of the male orgasm behaviour pattern curtailed because the sign stimulus releasing the rest of the pattern is not given by the female (see fig. 6).

(*b*) *Function of Quiver*

Since the male quiver appears to be the same in all situations it seems to us that its result depends only on the situations in which it occurs. For example, there are situations in which the male can be said to 'court' the female by quivering, and others in which the quiver may function as a threat to the female. Similarly, the quiver of male against male may be a threat. Fig. 5 shows the situations in which the male quiver is used, and its probable function.

It may be that a male can determine the sex of another fish only by its response to his quiver: the male quivers and the sex-characteristic response of the other fish determines his subsequent actitivity. For instance, when a male quivers against an active female she will give the typical female response 'cutting,' in which case he makes no further immediate movement. On the other hand, an intruding male responds to the male quiver by either moving away or remaining; in the latter case the intruder will

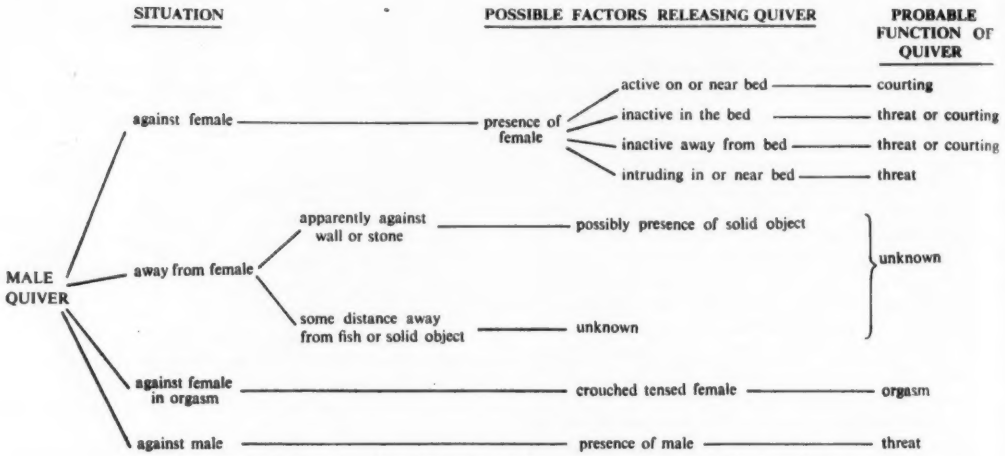


Fig. 5. The male quiver: situations in which it occurs and its probable functions.

be attacked. Similarly, a female failing to give the female response (cutting) will be attacked.

(*c*) *Origin of Quiver*

It is apparent that the significance of the male quiver is far from clear. We can at least surmise that the quiver evolved from the orgasm-quiver. In this connection it may be significant that the male salmon parr uses the quiver only rarely, and only then in the presence of the adult female and at the orgasm (Jones & King, 1950b, 1952). It seems probable that the attainment of sexual maturity in male salmon parr is comparatively recent, and that the evolution of the quiver in the parr has not yet reached the complex state found in the adult male.

2. The False Orgasm

Numerous false orgasms have been seen in both salmon and trout. In this operation the female crouches and the male darts alongside her in the bed, he quivers, and the female, remaining crouched, tenses and opens her mouth slightly; the male meanwhile opens his mouth and sometimes is seen to pass out a small amount of sperm. The female does not bend her body any further nor open her mouth wider as in the full orgasm, nor are any eggs passed out. She relaxes and rises from the crouch position and continues cutting and feeling. This activity suggests that the false orgasms occur because the female, at the very last minute, finds that the bed is not suitable for oviposition.

3. The Orgasm

The trout orgasm lasts for one to two seconds and that of salmon only about ten seconds. It is difficult, therefore, especially in trout, to follow the sequence of events. However, the occurrence of false orgasm shows that there is a chain of interrelated stages in the stereotyped pattern of the normal orgasm which can be interrupted before consummation. A tentative analysis of this sequence is presented diagrammatically in fig. 6.

In the above chain of events it is probable that (*a*) the crouch position, (*b*) the crouch position + open mouth are sign stimuli which respectively release (*a*) the forward dart and quivering of the male and (*b*) the beginning of ejaculation.

On one occasion in salmon and another in trout the female, when completely alone, the male having just left her, carried out several times in succession the actions included in the box in Fig. 6. Each time she rose from the bed after (6) and, without any cutting or feeling, crouched and repeated the sequence (1), (4), (6). After four or five such uncompleted spawnings, she was rejoined by the male and complete orgasm took place immediately. This suggests, as indicated in the diagram, that the sign stimuli releasing the female actions (1), (4) and (6) are not supplied by the male but are part of the situation 'bed suitable for orgasm.' The presence of the male appears to be necessary beyond stage (6), and the stimuli releasing female action (8) are contained in the situation 'bed finally suitable + male present alongside.'

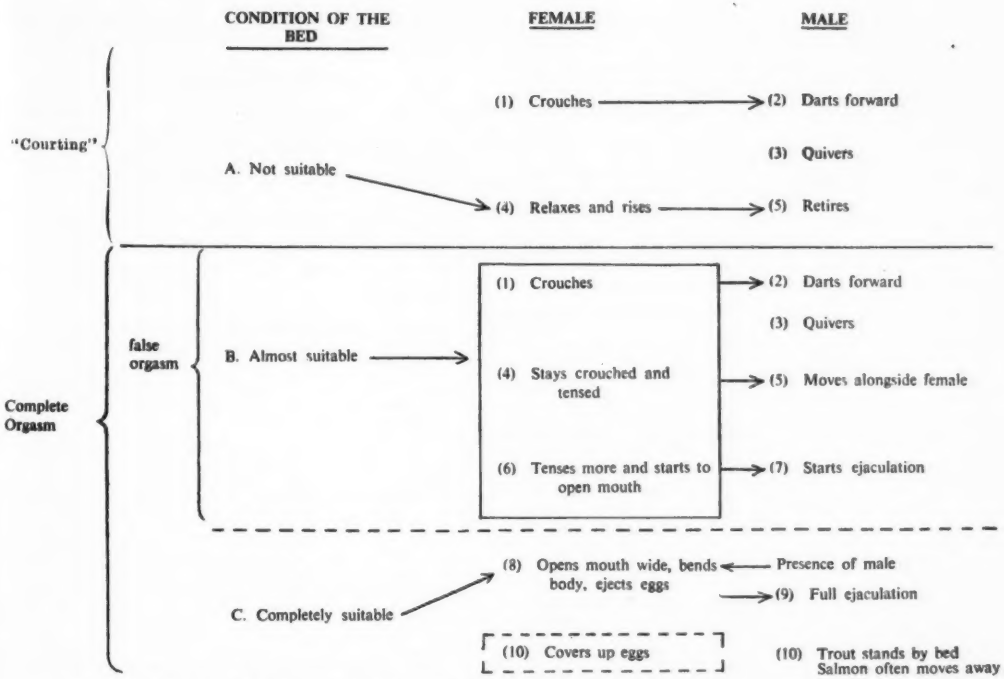


Fig. 6. An analysis of the orgasm behaviour of salmon and trout. Arrows indicate casual relationships; the numbers in brackets indicate the chronological sequence of events.

In some false orgasms no sperm was actually seen, but this may only mean that very little was ejaculated. The emission of sperm in some, (possibly all) false orgasms may be interpreted in one of two ways: (*a*) Sperm ejaculation takes place in one stage and is released by the sign stimulus: widely opened mouth + bent tensed body of the female, which occurs only in true orgasm (see fig. 6). Sperm emission in some false orgasms, in the absence of the sign stimulus, indicates exceptionally high motivation of the male mating drive and could be regarded as a vacuum activity. (*b*) Sperm ejaculation takes place in two stages, the start of ejaculation being released by a crouched female with partly opened mouth, and the continued ejaculation by a crouched female with tensely bent body and widely opened mouth.

The second interpretation appears to us the more likely, since in several false spawnings sperm was seen coming from a male which had spawned five times in the previous seven days, and in which, therefore, the mating drive was probably not exceptionally highly motivated. The diagram above was constructed with this interpretation in mind.

It is realised that until each of the causal relations indicated by arrows in the diagram has been shown actually to exist, by means of tests with dummies, the above analysis cannot be regarded as more than a hypothesis, probably true in view of the evidence from false orgasm and the behaviour of the females attempting to spawn alone, but not actually proved. We believe, however, that the production of this first analysis is useful at this stage in forming a suggestive basis for future correction and improvement.

VIII. An Examination of the Redds Made in the Trout Tank

Four of the redds made in the tank were examined. Redds 1, 2 and 3 were made successively by a three-year-old female and contained 233, 220, and 141 eggs respectively. The eggs

were found in packets about 2½ inches below the normal gravel surface (Plate II, 2). The fourth redd examined was the first one made by another three year old female and contained 307 eggs 3 to 4 inches below the gravel surface. In every case most of the eggs were found under one or two larger pieces of gravel (Plate II, 1): salmon eggs are similarly protected. Ninety-nine per cent. of the eggs had been fertilized.

In order to demonstrate that the female trout succeeds in excavating a hole in the gravel at the bottom of which there is almost no movement of water, the following experiment was carried out.

As soon as a female had spawned she was removed from her bed. The spawning in which she had partaken had been normal, in that no eggs were carried out of the bed by water currents. A suspension of Hyflo Super-Cel was squirted into various regions of the bed and a cine film was taken as each pipette-full dispersed. It is seen clearly in the film that when the suspension was introduced at the bottom of the bed just above the two large stones, much of it settled down between these stones and was not dispersed by currents. When introduced about three inches above the bottom of the bed most of the suspension was carried downstream. It would thus appear that the female trout does succeed in producing a depression at the bottom of which there is comparatively little movement of water. The experiment did not show the presence of a downward current at the bottom of the bed.

Summary

1. By using specially constructed tanks it has been possible to observe in detail and take cine films of thirteen spawnings of brown trout, and over eighty spawnings of the salmon. Despite the artificial conditions in which these fish spawned we believe that their spawning behaviour, as observed, was normal.
2. A detailed description is given of the behaviour of the fish throughout the spawning act.
3. The spawning behaviour is analysed and the possible significance of the various activities is discussed. It is shown that the orgasm can be regarded as a short reaction chain.
4. An experiment was made to demonstrate the currents in the bottom of a bed in which a female had spawned. Several redds were examined.

Acknowledgments

We are very grateful to Mr. S. Drinkwater for constructing the tank and making the pump, and to Professor R. J. Pumphrey, F.R.S., for valuable advice and criticism; to Mr. W. Lee for taking excellent still photographs; to the Welsh Land Sub-Commission for permission to catch trout from their waters, and to Mr. Stevens, of Chirk Fish Hatchery, for supplying suitable trout.

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Symposium: Behaviour and the Nervous System

This Symposium was held in the Department of Psychology, Birkbeck College, Malet Street, London, W.C. 1, on 18th February, 1954, under the auspices of the Association for the Study of Animal Behaviour. The following papers were presented.

SOME NEUROPHYSIOLOGICAL PROBLEMS RAISED BY ETHOLOGY

By N. TINBERGEN

Department of Zoology and Comparative Anatomy, Oxford

Just as in any other domain of biology, the biological study of behaviour is concerned with three major problems: that of the survival value, or functions of the observed phenomena; that of their causation; and that of their evolutionary history. For the present discussion I will have to restrict myself to some aspects of causation, that is, of the physiology of behaviour.

As I argued in my book "The Study of Instinct" (1951), a full understanding of the causation of behaviour will be possible only if specialists in the various fields concerned (neurophysiology and anatomy, sensory physiology, endocrinology, ethology, etc.) will seriously try to bridge the gaps which still exist between these fields. In trying to close these gaps, and thus to proceed towards one comprehensive science of animal movement, it is essential to carry out analyses on every integrative level of the organisational hierarchy. These analyses have to proceed step by step, and not a single level can be left unstudied. There is a tendency, particularly among those colleagues working on the lower integrative levels, to ignore the levels now being studied by ethologists, and to try to arrive at an understanding of the causation of behaviour by jumping to sweeping conclusions based upon knowledge (physiological or anatomical) of phenomena at the level of the neurone, or of simple neurone systems. This attitude, often due to a failure to see the very real problems raised by ethology, is, in my opinion, extremely harmful to a sound development of a biology of behaviour.

The general method of study is, or ought to be, the same for all the integrative levels involved, although, naturally, each level requires its special techniques. The traditional distinction between "physiology" of sense organs, nervous system, effector organs, and the simplest types of their combined action on the one hand, and that part of ethology which is concerned with underlying causation on the other hand, is historically determined. But it is an artificial and outdated one, which tends to hamper research. "Ethologists" and "neurophysiologists" differ, or ought to differ, with respect to the level of the observed phenomena only, and not in any other respect. They are representatives of one science, and barriers between them should not be put up, but broken down. However, this removal of barriers, and the building, instead, of bridges between physiology and ethology, have to be done carefully, and will take a long time.

Ethology is still a young science. In an excusable eagerness to link up with other sciences concerned with animal movement (an eagerness which for too long has met with indifference on the part of those other sciences) ethologists have admittedly made some premature suppositions. This happens to every science. Criticism of these mistakes is of course necessary and valuable, but it is valuable only if based on a full knowledge of the main ethological literature. The time has gone when the study of behaviour was an easy playground for everybody, where incidental and superficial knowledge was considered a sufficient justification for an opinion. At the moment, in a stage of rapid maturation of ethology, no one ought to close his eyes to the fact that it studies phenomena which have long been insufficiently investigated, and for the greater part totally unknown. Ethology can already be helpful in pointing to a number of problems, the study of which is only in its beginning.

Of these problems, the following were briefly discussed: the filter function involved in the responses to "sign stimuli"; the synthetic process of integrating sensory data to configurational stimulus situations; those processes of waning of a response which are not due to learning; the priming, releasing, and the blocking functions of stimuli in a chain of activities; the mutual suppression which two instincts, when activated, exert upon each other; the phenomenon of displacement activities.

THE FUNCTION OF THE CORPORA PEDUNCULATA IN BEES AND ANTS

By D. M. VOWLES
Cambridge

In the dorsal region of the protocerebrum in insects a group of association neurons is found, which has no direct connections with either sensory or motor organs. These groups of cells are called mushroom bodies or corpora pedunculata, and reach their highest degree of differentiation in the Hymenoptera. Comparative studies of the corpora pedunculata give no clue as to the function of these lobes.

A preliminary experimental study of their function has been carried out in various species of ants and in the Honey-Bee. The technique has been to damage various parts of the mushroom bodies, using a cautery, and to examine the subsequent effect on the behaviour of the insect. Two such effects on behaviour have been isolated and studied, although other unobserved effects may have occurred; these two effects are :

1. Continuous circling (both in flight and walking) to the intact side.
2. The loss of control and sensitivity of the antenna on the operated side.

These two effects have also been confirmed by the use of locally applied excitatory drugs (anticholinesterases). In ants, both effects were further localised: circling was only caused after damage to the medial calyx, while the antenna was affected only after damage to the lateral calyx. Damage to the α Lobe produced similar but much more variable results. In the Honey-Bee the same two effects were observed, but they could not be specifically referred to either calyx, and damage often caused no observed changes in behaviour.

Studies on the histology of the corpora pedunculata revealed that they had three main lobes—the calyces, the α Lobe and the β Lobe. The calyces and α Lobe both receive connections from all the sensory centres of the brain. The β Lobe gives connections to the motor centres. Each neuron in the corpora pedunculata has three branches—to the calyx, the α Lobe and the β Lobe: within these lobes they end, and make synaptic connections with association neurons from the rest of the brain. It was suggested that excitation passing in at the calyx and the α Lobe would interact, and that the excitation passing down the β Lobe and thence to motor centres would be the result of this interaction.

NERVOUS ANATOMY AND BEHAVIOUR PATTERNS

By J. E. SMITH
London

HORMONES IN THE NEURAL ANALYSIS OF BEHAVIOUR

By W. S. BULLOUGH
London

THE IMPORTANCE OF NEURAL ANALYSIS IN THE STUDY OF ANIMAL BEHAVIOUR

By J. Z. YOUNG
London

Symposium: Genetics and Behaviour

This Symposium was held in the Galton Laboratory, University College, London, on 22nd April, 1954, under the auspices of the Association for the Study of Animal Behaviour. Abstracts of the papers presented are given below.

GENETICAL INFLUENCES ON HUMAN BEHAVIOUR

By L. S. PENROSE

University College, London

Unlike psychology and physiology, genetics is concerned with differences between members of the same species. These are differences which are usually neglected deliberately in the normative sciences.

Nevertheless, human behaviour differences within the normal range are known, which are due to single genes; some of them are detected entirely by observing behaviour, for example, colour blindness and phenylthiourea taste deficiency.

Less exactly understood, but probably also much influenced by one or more genes, are differences in special abilities. For example, aptitudes for music, mathematics, languages. The genetical analyses of behaviour differences due to intelligence level and temperamental traits lead to conclusions even less precise though intra-familial likenesses are very significant.

Abnormal human behaviour can be determined by single genes; for example, deaf mutism phenylketonuria and microcephaly. Abnormal temperaments and anti-social traits must usually be attributed to the interaction of environment with a variety of genetical influences, a complex in which the components are very difficult to separate.

With experimental animals, behaviour differences due to single genes are most easily demonstrated when there are correlated morphological changes. Multiple gene differences are demonstrable by selective breeding of animals for special skills or temperaments. These results are in agreement with those inferred from human studies.

BEHAVIOUR IN CATTLE WITH SPECIAL REFERENCE TO TWINS

By H. P. DONALD

Animal Breeding Research Organisation, Edinburgh

Comparison of the performances of one-egg and two-egg twin cattle with pairs of half-sibs—all reared together under uniform treatment—indicates that the half-sib pairs have a greater intra-pair variability than would be expected from the purely additive genetic relationships involved. This increased variability appears to develop with age and consequently the fact that each pair of twins had one dam and each pair of half sibs had two does not seem to offer a likely explanation, especially with characters like weight at 18 months of age or date of emergence of permanent incisor teeth which are so far removed from a maternal influence. An alternative explanation might reside in genotype-environment inter-action. Observation of cattle suggests many ways in which they differ in their reaction to or interpretation of the same physical environmental factors. Concordance of one-egg twins in at least some of these ways suggests that reactions are genetically determined. Examples of differences in reaction occur in respect of sucking (of ears, teats), let-down of milk, and grazing habits. Owing to their genetic divergence and lack of prenatal vascular anastomosis, half-sister pairs have more opportunity to develop differences in reaction to, or choice of, environment and this may be reflected in increased intra-pair variation. The point seems worth further study in order to find out whether attention needs to be devoted in breeding to adaptation to present and future herd environments.

THE GENETICAL DETERMINATION OF BEHAVIOUR

By J. B. S. HALDANE
University College, London

The paper was mainly devoted to the work of Rendel (1945) and Koopman (1950) on *Drosophilia* species and of Sheppard (1954) on the moth *Panaxia dominula*, with an account of some unpublished observations by Hollingsworth in my own laboratory. Each of two gene differences analysed (normal *vs. yellow* in *Drosophila* and normal *vs. bimaculata* in *Panaxia* affected both sexes. Normal females are much less prone to mate with yellow males than with normal males, which yellow females show no preference. And matings between members of different genotypes of *Panaxia* are more frequent than between those of the same genotype.

The behaviour of *Drosophila* females can rapidly be changed by selection. Rendel produced a stock of normal females which accepted yellow males, and Koopman produced a stock of *D. persimilis* females which repelled *D. pseudoobscura* males, whereas the original stock accepted them. The nature of the signals, and the bearing of these results on current theories of behaviour, were discussed.

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"BEHAVIOUR" MUTANTS IN THE MOUSE

By HANS GRÜNEBERG
University College, London

The author gave a brief description of the behaviour of a group of mutant characters in the house mouse with structural anomalies of the labyrinth. All these mutants show a characteristic triad of symptoms consisting of circular movements, head tossing and deafness (except the mutant fidget which can hear); most of them also cannot swim. In five mutants of this group (waltzer, shaker-1, shaker-2, jerker and Varitint-waddler), the gross structure of the labyrinth is normal; degenerative processes in the neuro-epithelia and ganglia of the labyrinth take place early or late in post-natal life. In another group of such mutants (shaker-short, kreisler, dreher, fidget) there are various gross anomalies of the labyrinth (absence or reduction of semicircular canals, cyst formations etc.) which arise early in embryonic life when the labyrinth is first formed. In the mutant pallid, minor postural anomalies are associated with absence of otoliths. There also exists a large group of neurological mutants with a variety of neurological symptoms; these include the genes for jittery, wobbly, wabbler-lethal, Trembler, reeler, dilute-lethal, tremor, agitans, vacillans and many others; in the majority of them the anatomical substrate of the abnormal behaviour is not yet known. The behaviour of some of these mutants was illustrated by living material and a film produced by D. S. Falconer (Edinburgh).

Book Reviews

Bird Study: *The Journal of the British Trust for Ornithology*. Vol. I, No. 1, March, 1954. Business Editor: BRUCE CAMPBELL, B.T.O., 2, King Edward Street, Oxford. Annual subscription, £1 0s. 6d.

We welcome this new publication, which is in the capable editorial hands of H. N. Southern and which promises to fulfil the important task which it has been set. As Maj.-Gen. H. P. W. Hutson, Chairman of the B.T.O., points out in his foreword, progress in ornithology, as in every other science, is very dependent upon publication. While some field workers fail to record findings of value, others have a tendency towards over-publication, and both categories fail to attain their true objective, "to make known information as it is acquired and to do this without clogging the publication machinery with facts which fellow workers do not need."

The first issue contains papers on the breeding biology of the Greenfinch, by J. F. Monk, on two robin populations, by David Lack, and on "Back Garden Ornithology" by Peter Hartley, together with various B.T.O. items, including those relating to permanent enquiries, Trust-aided investigations and requests for information. The article by Hartley should help considerably those whose opportunities for field work are limited but who nevertheless wish to devote their time to the more serious aspects of bird-watching. We trust that this new publication will have a wide circulation and influence. A.N.W.

Feathered Wings. By ANTHONY JACK. London: Methuen, 1953. Pp. 124, plus selected bibliography and index. 15s.

A book on bird flight is always worth perusal when it is written by an experienced airman with an obvious sympathy for the living bird. It sometimes so happens that a writer, who is predominantly an airman, over-simplifies his interpretations of natural flight in assuming that the bird-wing acts as a more or less inflexible aerofoil rather than as a series of aerofoils presenting to the air-flow different angles of attack at the same time. The author of the present book cannot be accused of underestimating the complexities of the subject: he has misgivings about the limitations of applying the data obtained for the design of an aircraft wing to the bird-wing. "I am not a scientist and I am not in sympathy with the idea that the final word upon either flight or birds lies with science." However much the reader may feel inclined to disagree with this, it is a brave and honest statement of belief which no one can confidently criticise on the grounds of sound knowledge.

The study of bird-flight demands a familiarity with the principles of aerodynamics and the author explains to the reader what he believes to be a sufficiency of aerodynamical principle for the bird observer. Intentionally, he writes superficially. In the chapter on the theory of the aerofoil we read that "one can have an elementary grasp of how a bird flies without resolving the resultant force into components and the merits of simplicity are in this case greater than those of following the beaten track." He does mention the terms "lift" and "drag" but only to familarise his readers with their existence. Some may think that his account suffers as a consequence of too much simplification; on the other hand, as the book is written for bird-watchers with only a passing interest in flight, one cannot but agree that something must be sacrificed to make easy reading. Flapless flight is considered in a short chapter of about five pages; flapping flight in a chapter of eighteen. There is nothing in these chapters to which one can take exception and the treatment of each aspect of the subject follows the conventional lines. Other chapters are devoted to wind, wings, manoeuvres, aerobatics, albatrosses, anatomy, speed and height of flight, meteorology and navigation. The chapter on albatrosses contains fascinating accounts of the author's own observations. The book is readable and well-indexed; good line drawings are well designed to clarify the test and there are excellent photographs. From the point of view of flight, the value of the photographs would have been greatly enhanced by the addition of accompanying captions describing their aerodynamical significance. C.H.S.

WANTED : Bulletin of Animal Behaviour, No. 4. Reply to Librarian, University, Reading.

BIRD STUDY

The Journal of the British Trust for Ornithology

Edited by H. N. SOUTHERN

Contents of Vol. I, No. 2, (June, 1954) include *Loss of Rings in Marked Herring Gulls*, by R. H. Poulding; *Population Changes in Titmice, 1947-1951*, by John Gibb; *Ornithological Surveys of Nature Reserves, 1953*, by Bruce Campbell; *The Advertising Behaviour of the Great Crested Grebe*, by K. E. L. Simmons.

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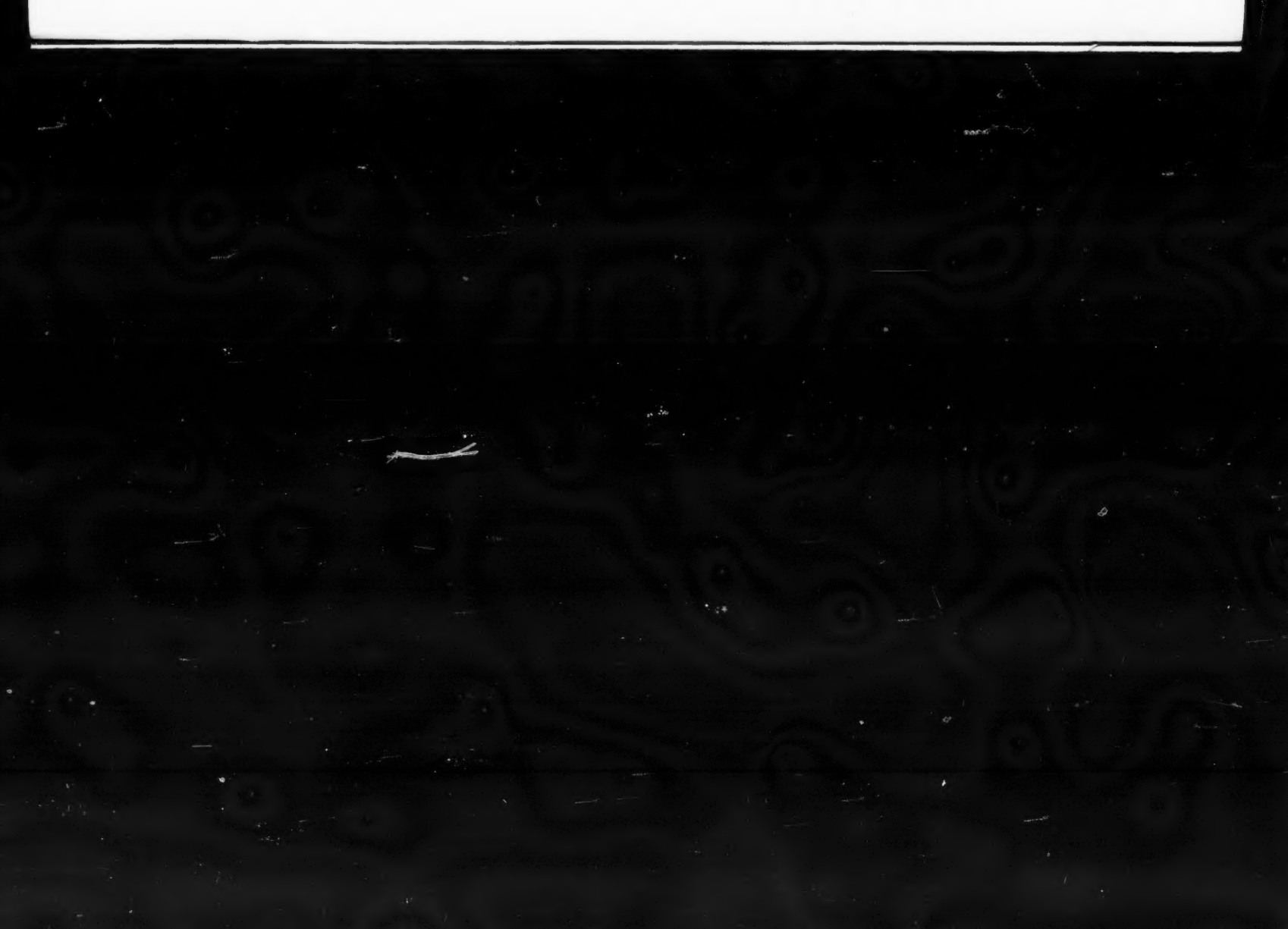

Association for the Study of Animal Behaviour

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OBJECTS

The Association for the Study of Animal Behaviour is a scientific society, founded in 1936. Its aim is to promote and co-ordinate work in animal behaviour, the study of which is of interest or importance to a wide range of biologists, e.g., those engaged in psychology physiology, zoology, animal husbandry and veterinary science.

Scientific meetings are held, often in conjunction with other societies, and the Association possesses a library from which members may borrow, and to which all members are asked to contribute copies of their publications. From 1936 to 1952 the Association published at irregular intervals the BULLETIN OF ANIMAL BEHAVIOUR. This has now been replaced by a regular quarterly publication, the BRITISH JOURNAL OF ANIMAL BEHAVIOUR, which contains original scientific papers and reviews.

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THE BRITISH JOURNAL OF ANIMAL BEHAVIOUR is published quarterly. Annual subscription 27s. 6d. U.S.A. and Canada, $5.00.

Printed by Rockwell Printers, Westford, Wellington, Som.